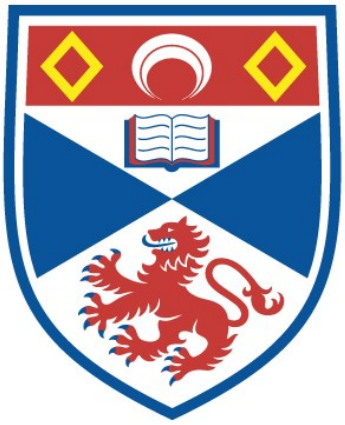
NEURAL MECHANISMS UNDERLYING THE PERCEPTION OF SOCIALLY RELEVANT STIMULI IN THE MACAQUE MONKEY

Amanda J. Mistlin

A Thesis Submitted for the Degree of PhD
at the
University of St Andrews



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"...but vether it's worth while goin' through so much to learn so little, as the charity-boy said ven he got to the end of the alphabet, is a matter o' taste." [Mr Weller]

Dickens Pickwick Papers (ch. 30)

CONTENTS

CHAPTER 5: Behavioural investigations into the importance of facial and body attributes, and motion, on social communication in macaque monkeys.

ACKNOWLEDGEMENTS

To David Perrett - for providing enough enthusiasm for the both of us, for his helpful if totally illegible comments on previous drafts of the manuscript, for caring and for bullying me into submission!

To the animal house technicians, especially Derek Brooks - whose assistance was often invaluable and gratefully appreciated. To Pete Frew, and the other technicians - who put up with my constant appearances in the workshop with good humour and the united cry of "here comes trouble".

To Alan Cowey and Charles Heywood - for enabling me to conduct experiments in the Department of Psychology, University of Oxford, and for their time and assistance.

To David Milner - for helpful comments on previous drafts.

To Mark, the two Andrews and Douglas - who helped provide light relief in the lab and distracted Dave at just the right times.

To Fiona - who gave more than expected, and taught me how to groom.

To both Janes and Frances - for not asking about the "achem", providing tissues, and for just being there when I needed a good moan.

And to all my friends who endured my moods and blues.

Finally, to my parents and family - without whose love and support I might not have made it.

ABSTRACT

Neural mechanisms underlying the perception of socially relevant stimuli in the macaque monkey.

Present knowledge indicates the importance of one region of monkey temporal association cortex, the superior temporal sulcus (STS), in predominantly high level analysis of 'biologically' important objects. To clarify and elaborate on the function of the monkey STS, the following questions are addressed: (1) what kind of tactile processsing occurs in the polymodal STS and does it compare with the complex visual processing observed; (2) does behavioural sensitivity to face and body information parallel neural sensitivity (of STS cells) to the same stimulus dimensions; (3) does monkey STS ablation result in a behavioural indication of impairments in the perception of socially relevant stimuli; and (4) are visual cells in the STS sensitive to social communicational elements of facial or postural expression? Single-unit recording studies of the macaque STS (using standard techniques in awake, behaving animals) reveal a population of somatosensory neurones, with large receptive fields, sensitive only to unexpected (unpredictable) tactile stimulation. Complex tactual-visual interactions observed stress the importance of this dimension of processing. A separate population of visual cells exhibit sensitivity to compound facial expressions and head/body postures important in primate social communication. A behavioural study of monkeys' socio-emotional responses to configurational aspects of faces, the posture of the head and the interaction of form and

motion, reveal their ability to discriminate salient cues in the context of social communication/interaction. It is tentatively shown that monkeys with the STS ablated are unable to make such discriminations, so reacting inappropriately to the stimuli (a symptom of Kluver-Bucy syndrome). The combined findings show that the STS performs a multimodal perceptual analysis of socially relevant stimuli, and suggest that the STS provides a sensory input to a limbic structure, such as the amygdala, through which it mediates appropriate emotional reactive behaviour.

CHAPTER 1

Introduction to the study of perception and the role of the superior temporal sulcus in the monkey.

1.1 Introduction

The association areas of the cerebral cortex, being relatively remote from peripheral sensory input and direct motor output, are presumed to subserve 'complex', integrative neural functions such as thought, perception, learning, planning and interpretation of communicative signals, attention and consciousness. Although these functions have been extensively studied in their own right - through the acquisition of electrophysiological, clinical and behavioural data - the role of specific association areas in these functions remains unclear.

The concern of this thesis is one region of the temporal association cortex known as the superior temporal sulcus (STS) which has only come under intensive investigation in the last few years; despite the emergence of its involvement in the perception of biologically important stimuli (Baylis et al, 1985; Bruce et al, 1981; Desimone et al, 1984; Gross et al, 1972; Leonard et al, 1985; Perrett et al, 1982, 1984, 1985a,b, 1987a,b; Rolls et al, 1985). The fundamental importance of this perceptual faculty is self-evident and yet neurone involvement in, or specialization of, a small region of the brain for this neural function remains speculative. This piece of work was

directed therefore to understand further the role of the STS in perception, where perception is defined following Bruce and Green (1985) as the combination of different sensations and the utilization of past experience in recognizing the objects and facts from which the present stimulation arises. (It is not within the scope of this work to debate the merits of this definition; a concise overview of the different perceptual theories is given in Bruce and Green (1985).)

In attempting to understand the neural mechanisms underlying perception, one must conclude that such activities necessitate a considerable degree of convergence and integration of all sensory systems (Adrian, 1949; Fessard, 1954). Jones and Powell (1970) identified the STS as one such discrete site of convergence. Since this discovery a variety of disciplines relating to the study of the brain's functions have contributed independently to our still limited knowledge of the STS's functions.

Connectional studies have contributed not only to identifying the multimodal nature of the STS cortex (Chavis and Pandya, 1976; Jones and Burton, 1976; Jones and Powell, 1970; Pandya and Seltzer, 1982; Seltzer and Pandya, 1978, 1984) but hint at the functional role of the STS by virtue of its input/output pattern of connections. It is understood that the STS receives cortical inputs from unimodal regions of sensory cortex such as the inferior temporal cortex whose neurones are visual, the superior temporal gyrus whose neurones are auditory, insular cortex whose neurones are somatosensory (Friedman et al, 1986) and other inputs from cortical areas that are themselves polysensory - the posterior parietal cortex, the lateral frontal cortex,

orbitofrontal cortex, cingulate gyrus and the parahippocampal gyrus (Jacobsen and Trojanowski, 1977; Jones and Burton, 1976; Jones and Powell, 1969, 1970; Pandya and Kuypers, 1969; Pandya and Yeterian, 1985). Reciprocal projections exist between the STS and the majority of these multi-sensory regions of cortex.

Electrophysiological evidence has substantiated the polysensory nature of the STS (Benevento et al, 1977; Bruce et al, 1981; Perrett et al, 1985b), but indicates a visual modality dominance, and has revealed discrete populations of neurones selectively responsive to complex stimuli such as faces and bodies (Baylis et al, 1985; Bruce et al, 1981; Desimone et al, 1984; Gross et al, 1972; Leonard et al, 1985; Perrett et al, 1982, 1984, 1985a,b, 1987a,b). From Gross et al's (1972) primary observations of a few cells in macaque temporal cortex responding selectively to the visual stimulus of an upright monkey's paw to the more detailed reports (e.g. Perrett et al, 1982, 1984, 1985a,b, 1987a,b) of populations of cells in the STS activated by complex interactions of form (primate faces and bodies) and motion (along axes generally centred on the observer), it has become increasingly clear that the monkey STS has some involvement in a high level of (polysensory?) processing of socially relevant stimuli.

This high level involvement of the STS, in face processing in particular, has led to the suggestion that damage to an area homologous to that of the STS in the macaque could be responsible for the neuropsychological condition known in man as prosopagnosia (face non-recognition). [An anatomical and neurobehavioural description of prosopagnosia is given in Damasio et al (1982).] It appears that the

presence of an anatomically defined subsystem (Perrett et al, 1984) within the STS that processes faces is in accordance with the view that prosopagnosia involves a selective disturbance of a face processing system (Perrett et al, 1987b). However there are other types of cell in the STS sensitive not just to faces but to actions and body movements (Chitty et al, 1987; Perrett et al, 1985a) hence it seems unlikely that prosopagnosia (if resulting from damage to an area such as the STS) could occur in the complete absence of any other visual processing deficit. Indeed prosopagnosia is rarely seen in isolation, as the likelihood of a discrete lesion to a region within an area such as the STS occurring naturally would be rather low.

Following specific lesions to the STS polysensory cortex (in monkeys) no impairments on standard visual discrimination or recognition tasks have been reported (Aitken, 1980; Ettlinger and Garcha, 1980; Petrides and Iverson, 1979), which proves only that the STS's functions lie beyond the 'simple' processing of sensory information. Impairments in terms of a behavioural response have, however, been reported with STS lesions (Luh et al, 1986). The effect on emotional responsiveness hints at another role for the STS - in controlling affective behaviour or its neural mechanisms. Connectional data tentatively supports this hypothesis in that the STS sends (and receives) a heavy projection to the limbic system, particularly the amygdala (Aggleton et al, 1980; Aggleton and Passingham, 1981; Jones and Burton, 1976; Jones and Powell, 1969, 1970). It is interesting to note that visual hypoemotionality has been reported in prosopagnosic patients with bilateral temporal-occipital brain damage (Bauer, 1982; Habib, 1986).

So, our present knowledge indicates the importance of the STS predominantly in high level analysis of biologically important objects; and suggests an associated role in attaching emotional significance to a stimulus or event. The work presented here stems from this base, primarily developing those findings of Perrett et al (1982, 1984, 1985a,b) in the electrophysiological field and challenging those lesion studies that have found no perceptual impairments following the removal of the STS. The specific questions addressed in this treatise are outlined below.

(1) Processing of what kind of tactile information occurs in the polymodal STS and does it compare with the high level processing observed for visual sensory information?

To date studies have concentrated mostly on a representation of the visual modality (and to some extent the auditory modality) in the STS. Despite the polymodal nature of the STS and the recent discovery of a pure somatosensory input to the STS from the insular cortex (Friedman et al, 1986) time has not been found to fully investigate the tactile properties of cells in this association cortex. It might be expected that tactile processing proceeds to the same complex level as visual processing in the STS considering Mishkin's (1979) proposal that visual and tactile processing pathways in the brain are subserved by analogous regions of sensory (and association?) cortex.

(2) Does behavioural sensitivity to face and body information parallel neural sensitivity (of STS cells) to the same stimulus dimensions?

Visual single unit studies of the STS have revealed a high degree of specialization in the categories of stimuli processed (e.g. Chitty et al, 1987; Perrett et al, 1982, 1984, 1985a,b, 1987a,b). This success in categorization of cell types was partly due to the novel approach of presenting natural stimuli to the subject presumed to be behaviourally relevant in a monkey's social environment e.g. faces of monkeys, expressive body movements, etc. Although the use of such stimuli was guided to some extent by primate behavioural repertoires (Bertrand, 1969; Chance, 1962; Hinde and Rowell, 1962; van Hooff, 1962), there is little documentation of behavioural sensitivity to certain face and body attributes such as facial configuration and body posture.

(3) Does removal of the STS cortex from a monkey result in any behavioural indication of an impairment in the perception of, or reaction to, socially significant stimuli?

Previous STS lesion studies investigating performance on visual tasks were restricted to 'simple' stimuli, which perhaps not surprisingly were unsuccessful in identifying visual discrimination impairments considering the physiology and nature of objects for which the STS seems specialized. Noting alteration in affective behaviour following such STS lesions in the report of Luh et al (1986) it seems reasonable to propose that either a recognition deficit for face-like material or a change in emotional responsivity might accompany an STS lesion. Evidence of such deficits would indicate the <u>essential</u> role of the STS in the processing of socially relevant stimuli.

(4) Are cells in the STS visually sensitive to the 'true' communicational elements of facial or postural expression inherent in primate social communication?

Perrett et al (1982, 1984, 1985a,b, 1987a,b) have formed an extensive catalogue of cells in the STS that code many aspects of the primate face and body (such as the presence of individual facial features, face configuration and head view) that might be utilized in social communication. Considering this one might expect within the STS, at the cellular level, manifestations of the coding of more direct expressive forms and gestural signals, e.g. submissive/threat faces or body attitudes.

A true understanding of the functions of the STS cannot be achieved by focusing on one aspect of STS coding alone, or on one method of assessment; a unified approach is needed in which specialized methods are applied in a coordinated way to solve the distinct but related questions. For this study, common electrophysiological methods (Chapter 2) were employed to answer both questions 1 (Chapters 3 and 4) and 4 (Chapter 7) where the aim was to identify the trigger features (both tactile and visual) of individual STS neurones. Questions 2 and 4 were intimately related in that testing methods developed for the behavioural study of monkeys' responses to faces, bodies and expressive postures (Chapter 5) were utilized as a diagnostic tool for identifying behavioural deficits in the STS lesion study (Chapter 6). All experiments shared the premise that since stimuli with which an organism usually deals are not simple, there is no reason to assume that neural organization has evolved to deal with

such stimuli either (Lettvin et al, 1959); hence realistic, complex objects appropriate to the monkey were employed as stimuli to answer the said questions.

Each question is treated as a separate chapter, covering the practical aspects of the experiments involved and placing the work in the appropriate perspective. (There is no significance to the order in which the chapters are presented.) The implications collated from the results of the complete work are expressed in the final discussion of Chapter 7. It is left only to say that the aim of this thesis is to expand and substantiate knowledge of the functions of the superior temporal sulcus; it's hoped that this research goes some way towards fulfilling this aim, whilst inducing some excitement and interest in the patient reader.

1.2 References

Adrian,E.D.. (1949) "The Sherrington Lectures. I. Sensory Integration." University Liverpool Press, Liverpool.

Aggleton, J.P., Burton, M.J., and Passingham, R.E. (1980) Cortical and subcortical afferents to the amygdala of the rhesus monkey (Macaca mulatta). Brain Res. 190:347-368.

Aggleton, J.P., and Passingham, R.E. (1981) Syndrome produced by lesions of the amygdala in monkeys (Macaca mulatta). Comp. Physiol. Psychol. 95:961-977.

Aitken, P.G. (1980) Lesion effects on tactual to visual cross-modal matching in the rhesus monkey. Neuropsychologia 18:575-578.

Bauer, R.M. (1982) Visual hypoemotionality as a symptom of visual-limbic disconnection in man. Archs. Neurol. 39:702-708.

Baylis, G.C., Rolls, E.T., and Leonard, C.M. (1985) Selectivity between faces in the responses of a population of neurons in the cortex in the superior temporal sulcus of the monkey. Brain Res. 342:91-102.

Benevento, L.A., Fallon, J.H., Davis, B., and Rezak, M. (1977) Auditory-visual interaction in single cells in the cortex of the superior temporal sulcus and the orbital frontal cortex of the macaque monkey. Exp. Neurol. 57:849-872.

Bertrand, M. (1969) The behavioural repertoire of the stumptail macaque. Bibliotheca Primatologica no.11. Karger, Basel.

Bruce, V., and Green, P.R. (1985) Visual Perception: Physiology, Psychology and Ecology. Lawrence Erlbaum Associates, Hillsdale, New Jersey.

Bruce, C., Desimone, R., and Gross, C.G. (1981) Visual properties of neurones in a polysensory area in superior temporal sulcus of the macaque. J. Neurophysiol. 46:369-384.

Chance, M.R.A. (1962) An interpretation of some agonistic postures: The role of "cut-off" acts and postures. Symp. zool. Soc. Lond. 8:71-99.

Chavis, D.A., and Pandya, D.N. (1976) Further observations on corticofrontal connections in the rhesus monkey. Brain Res. 117:369-386.

Chitty, A.J., Perrett, D.I., Mistlin, A.J., and Harries, M. (1986) Visual cells sensitive to biological motion (in prep).

Damasio, A.R., Damasio, H., and van Hoesen, G.W. (1982) Prosopagnosia: Anatomical basis and neurobehavioural mechanism. Neurol. 32:331-341.

Desimone, R., Albright, T.D., Gross, C.G., and Bruce, C. (1984) Stimulus-selective responses of inferior temporal neurons in the macaque. J. Neurosci. 4:2051-2062.

Ettlinger, G., and Garcha, H.S. (1980) Cross-modal recognition by the monkey: The effects of cortical removals. Neuropsychologia 18:685-692.

Fessard, A.E. (1954) Mechanisms of nervous integration and conscious experience. In: J.F. Delafresnaye (ed.) Brain Mechanisms and Consciousness. Blackwell, Oxford, pp.200-236.

Friedman, D.P., Murray, E.A., O'Neill, J.B., and Mishkin, M. (1986) Cortical connections of the somatosensory fields of the lateral sulcus of macaques: Evidence for a corticolimbic pathway for touch. J. Comp. Neurol. 252:323-347.

Gross, C.G., Rocha-Miranda, E.E., and Bender, D.B. (1972) Visual properties of neurons in inferotemporal cortex of the macaque. J. Neurophysiol. 35:96-111.

Habib, M. (1986) Visual hypoemotionality and prosopagnosia associated with right temporal lobe isolation. Neuropsychologia 24:577-582.

Hinde, R.A., and Rowell, T.E. (1962) Communication by postures and facial expressions in the rhesus monkey (Macaca mulatta). Proc. zool. Soc. Lond. 138:1-21.

Jacobsen, S., and Trojanowski, J.Q. (1977) Prefrontal granular cortex of the rhesus monkey. I. Intrahemispheric cortical afferents. Brain Res. 132:209-233.

Jones, E.G., and Burton, H. (1976) Areal differences in the laminar distribution of thalamic afferents in cortical fields of the insular, parietal and temporal regions of primates. J. Neurol. 168:197-248.

Jones, E.G., and Powell, T.P.S. (1969) Connexions of the somatic sensory cortex in the rhesus monkey. I. Ipsilateral cortical connexions. Brain 92:477-502.

Jones, E.G., and Powell, T.P.S. (1970) An anatomical study of converging sensory pathways within the cerebral cortex of the monkey. Brain 93:793-820.

Leonard, C.M., Rolls, E.T., Wilson, F.A.W., and Baylis, G.C. (1985) Neurons in the amygdala of the monkey with responses selective for faces. Behav. Brain Res. 15:159-176.

Lettvin, J.Y., Maturana, H.R., McCulloch, W.S., and Pitts, W.H. (1959) What the frog's eye tells the frog's brain. Proc. Inst. Radio Engr. 47:1940-1951.

Luh, K.E., Butter, C.M., and Buchtel, H.A. (1986) Impairments in orienting to visual stimuli in monkeys following unilateral lesions of the superior sulcal polysensory cortex. Neuropsychologia 24:461-470.

Mishkin, M. (1979) Analogous neural models for tactual and visual learning. Neuropsychologia 17:139-151.

Pandya, D.N., and Kuypers, H.G.J.M. (1969) Cortico-cortical connections in the rhesus monkey. Brain Res. 13:13-36.

Pandya, D.N., and Seltzer, B. (1982) Association areas of the cerebral cortex. Trends Neurosci. 5:386-390.

Pandya, D.N., and Yeterian, E.H. (1985) Architecture and connections of cortical association areas. In: A. Peters and E.G. Jones (eds) Cerebral Cortex, Volume 4. Plenum Press, New York.

Perrett, D.I., Harries, M., Mistlin, A.J., and Chitty, A.J. (1987a) Three stages in the classification of body movements by visual neurones. In: H. Barlow, C. Blakemore and M. Weston Smith (eds) Images and Understanding. Cambridge University Press, Cambridge (in press).

Perrett, D.I., Mistlin, A.J., and Chitty, A.J. (1987b) Visual neurones responsive to faces. Trends Neurosci. 10:358-364.

Perrett, D.I., Rolls, E.T., and Caan, W. (1982) Visual neurones responsive to faces in the monkey temporal cortex. Exp. Brain Res. 47:329-342.

Perrett, D.I., Smith, P.A.J., Mistlin, A.J., Chitty, A.J., Head, A.S., Potter, D.D., Broennimann, R., Milner, A.D., and Jeeves, M.A. (1985a) Visual analysis of body movements by neurones in the temporal cortex of the macaque monkey: A preliminary report. Behav. Brain Res. 16:153-170.

Perrett, D.I., Smith, P.A.J., Potter, D.D., Mistlin, A.J., Head, A.S., Milner, A.D., and Jeeves, M.A. (1984) Neurones responsive to faces in the temporal cortex: Studies of functional organization, sensitivity to identity and relation to perception. Human Neurobiol. 3:197-208.

Perrett, D.I., Smith, P.A.J., Potter, D.D., Mistlin, A.J., Head, A.S., Milner, A.D., and Jeeves, M.A. (1985b) Visual cells in the temporal cortex sensitive to face view and gaze direction. Proc. Roy. Soc. Lond. B 223:293-317.

Petrides, M., and Iverson, S.D. (1979) Restricted posterior parietal lesions in the rhesus monkey and performance on visuospatial tasks. Brain Res. 161:63-77.

Rolls, E.T., Baylis, G.C., and Leonard, C.M. (1985) Role of low and high spatial frequencies in the face-selective responses of neurons in the cortex in the superior temporal sulcus in the monkey. Vis. Res. 25:1021-1035.

Seltzer, B., and Pandya, D.N. (1978) Afferent cortical connections and architectonics of the superior temporal sulcus and surrounding cortex in the rhesus monkey. Brain Res. 149:1-24.

Seltzer, B., and Pandya, D.N. (1984) Further observations on parieto-temporal connections in rhesus monkeys. Exp. Brain Res. 55:301-312.

van Hooff, J.A.R.A.M. (1962) Facial expressions in higher primates. Symp. zool. Soc. Lond. 8:97-125.

CHAPTER 2

General experimental methods for single unit recording in the macaque monkey.

2.1 Introduction

This chapter will describe the training procedures and general experimental methods used in this study for single unit recording in conscious macaque monkeys. Details of the methods used for particular experiments are presented in the methods section of later chapters.

2.2 Subjects

Recordings were made from two behaving rhesus macaque monkeys (Macaca mulatta). Both animals (one male, P, and one female, F) were received from Shamrock Farms at initial weights of approximately 3 kg. Over the recording period of one year for P and one and a half years for F, their weights increased steadily to 4.2 and 5.4 kg respectively. These monkeys were caged separately but housed with other monkeys.

A monkey was taken from its home cage and seated in a primate chair (see Figure 2.1) for the duration of an experiment (3-6 hours). Experiments were carried out on two or three days of the week over a

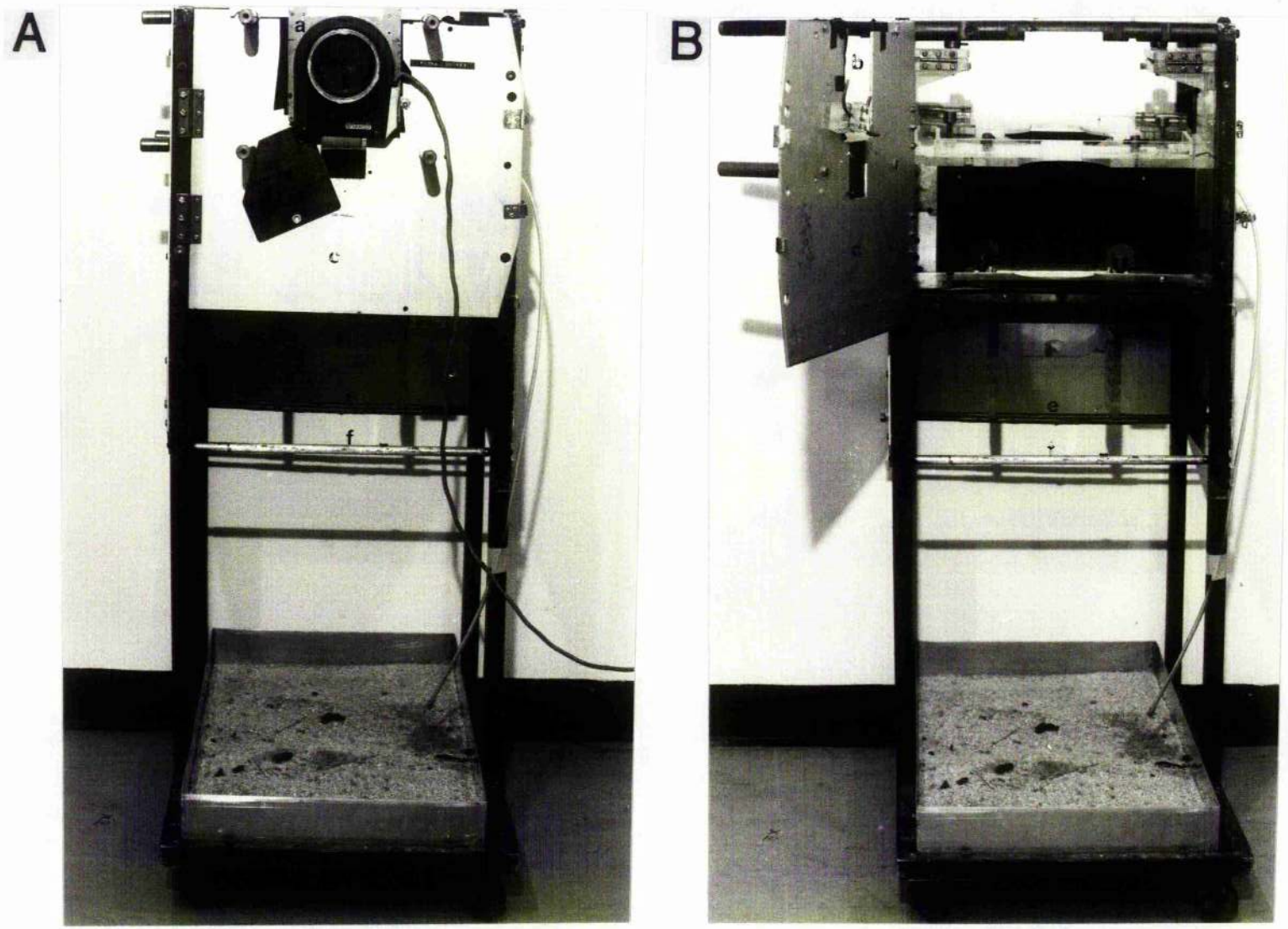


Figure 2.1 The primate chair used to seat and secure a monkey during cell recording. A, with the front panel closed; B, with the front panel open for somatosensory access to the monkey's torso. A visual aperture shutter (a) was laid over the monkey's viewing panel (b) in the front door (c) for somatosensory testing or timed presentations of visual stimuli. Below this, a hinged cover (d) reveals a panel through which the monkey could reach to palpate objects. The monkey rested on the seat (e) and feet (f) perches.

period of one to one and a half years. The monkey's head preparation was cleaned daily with a dilute antiseptic solution while the monkey sat in the primate chair. The subjects received 50-100% of their daily food and liquid intake during experimental sessions and were given ad lib food and water at the termination of each experiment. (Water deprivation of up to 24 hours was permitted under Home Office Licence, but this proved to a large extent to be unnecessary.)

2.3 Training

The monkeys were preoperatively trained for 1-2 months to get them used to the experimental set-up. For training they were seated in a primate chair for 30-60 minutes and fed by the experimenter. During this time the monkeys were trained on a visual discrimination task. The visual stimuli used in this task were presented to the monkey (for 1-2s) from behind a large aperture shutter which opened after a 0.5s signal tone. The monkeys were trained to lick a tube for sweetened water at the sight of real or pictorial faces (or any view of the head) but to withold lick response on trials with other stimuli.

During this training period a good working relationship was established between experimenter and subject. This was essential for investigations of somatosensory properties of cells which required a monkey to tolerate frequently being touched by the experimenter (see 4.2).

2.4 Implant Construction

Two stainless steel rings (16mm ID, 19mm OD, 10mm deep), designed to fit a David Kopf hydraulic micro-drive, were placed onto a sheet of glass overlying a fixed piece of graph paper. In this way the rings could be fixed relative to one another in appropriate positions with reference to two orthogonal axes which when positioned on the monkey's head would correspond to the saggital and interaural planes. For the final stereotaxic coordinates, the right ring (well) was centred 8mm and the left well 10mm anterior to the interaural plane; both wells were centred 12mm lateral to the saggital plane.

The edges of the rings were cemented to the glass plate with dental acrylate (Howmedica Int., London), care being taken that acrylic was not placed more than 2mm high on the walls of the rings, since this would interfere with the microdrive's subsequent positioning. Plastic tubes (7mm ID, 14mm OD, 61mm length) were placed in front of (approx. 38mm anterior) and behind (approx. 25mm posterior) the rings and cemented to them by a central line of acrylic which was placed around the centre of the tubes. (Horizontal bars could be inserted through these tubes and clamped to the sides of the primate chair for recording sessions, to ensure restraint of the head.)

When this construction was dry, it was floated off the glass with water and, in preparation for the following operation, placed in a stereotaxic holder (David Kopf Instruments, California) at predetermined antero-posterior coordinates. The laterality was

adjusted with respect to the midline saggital sinus.

2.5 Chronic Implantation

A rhesus monkey was sedated with intramuscular ketamine (Ketelar, 10 mg/kg, Park Davis and Co., Gwent) - a weight-dependent dosage - and then anaesthetized intravenously with 1-2ml of a barbiturate anaesthetic (Sagatal, 60mg/ml, May and Baker Ltd, Dagenham) until the cessation of the gabella reflex. 1.0ml atropine (0.6mg/ml, Evans Medical Ltd, Liverpool) was administered to reduce mucous secretion and 1.0ml dupocilin for protection from bacterial infection. The monkey's head was closely shaved and subsequently swabbed with alcohol and then iodine. A drop of paraffin oil was placed in each eye, the eyes then taped shut and the monkey placed securely into a David Kopf stereotaxic instrument. Full sterile precautions were then employed throughout the surgical procedures. Respiratory rate (30-40/min) and anaesthetic level were maintained constantly throughout the operation with additional anaesthetic being administered (when necessary) by intraperitoneal or intravenous injection.

The initial incision was made longitudinally along the skull, i.e. in the antero-posterior direction. The skin was reflected and a suitable area of skull cleared of connective tissue to the size of the implant. The implant (previously constructed, see 2.4), held at the preset coordinates in a stereotaxic arm, was then lowered to the skull and the size and position of the rings marked on the the skull; with the

implant raised the bone beneath the rings was removed. Following this the locations of the ring holes were checked and suitable positions on the skull were marked around the periphery of the implant for small holes for the insertion of stainless steel screws and T pieces. With the screws and T pieces locked in position (forming a firm frame to which the implant could be attached) the implant was lowered to sit flush with the skull and cemented in the preset antero-posterior coordinates calculated from a macaque stereotaxic atlas (Snider and Lee, 1961) and histological brain sections of rhesus monkeys of equivalent weights. P.E.P., a topical antibiotic (2% powder, Intervet Laboratories Ltd, Cambridge) was appplied to the exposed dura and plastic aerated caps fitted over the rings. The animal was subsequently removed from the apparatus and returned to its home cage where recovery occurred within a few hours. With these procedures the implant was stable throughout the recording period and showed no signs of infection even after one and a half years.

2.6 Recording Techniques

2.6.1 Electrode construction

Recording microelectrodes were constructed from 150mm straightened tungsten wire (125 microns OD) and fine capillary tubes of borosilicate glass (250 microns ID, 380 microns OD, 150mm length) using techniques adapted from Merrill and Ainsworth (1972). A piece of tungsten was electrolytically sharpened by repeatedly dipping one

end of the wire into Levick's solution (after Merrill and Ainsworth, 1972) while a voltage (2-3V) between this tungsten wire and a neutral carbon graphite electrode was maintained using a Regulac variable transformer (Claude Lyons Ltd, Herts.). When the tip was a suitable shape (discussed later), the wire was inserted (blunt end first) into a tube of insulating glass. The etched tip was drawn back 5.0cm inside the tube, its position marked on the glass and a drop of rapid-drying cyano-acrylic superglue (Loctite UK, Herts.) placed on the exposed end of the wire at the glass-wire boundary.

The microelectrode was then firmly secured in the electrode-pulling apparatus with the tip a fixed distance above a nichrome heating coil. Glass was then collapsed onto the metal electrode by passing a current through the coil and following this, glass insulation was stripped from the very tip of the electrode. This was achieved (under microscopic control) by inserting the electrode tip into a bead of solder glass, heated on a platinum-irridium wire, allowing it to cool and then removing the electrode tip from the bead.

Using a small volume of Levick's solution held in a glass capillary tube, the tungsten metal could be electrolytically re-etched (as above) if necessary, to a final tip shape approximately 6-10 microns wide and 10-25 microns long. The tip shape determined the electrode's performance and a trade-off was often necessary between a long, fine point for good (large signal to noise ratio), stable, single cell recordings and a shorter, blunter tip for durability in traversing brain tissue.

2.6.2 Electrode placement

Microelectrodes were advanced into the brain through a trans-dural guide tube (0.5mm ID, 1.0mm OD, 5cm length) using a David Kopf hydraulic micro-drive and micropositioner adapted to allow electrode passage at angles of 0-15 degrees with respect to vertical. The height at which the guide tube touched the dura was used as a fixed zero reference for calculating the depth of travel of the electrode into the brain. At the start of an experiment 0.1-0.2ml lignocaine hydrochloride (Xylocaine, 40mg/ml, Astra Pharmaceuticals Ltd, Kings Langley) was applied to the dura topically before inserting the guide tube 3-5mm through the dura. The microelectrode was lowered by hand to a predetermined distance below the dura, judged from X-ray measurements to be approximately the depth of the temporal cortex. At this depth the electrode was attached to the microdrive using poster adhesive (Blu Tak, Bostick Ltd, Leicester) and advanced or retracted in 10 micron steps, using the hydraulic system, to investigate the temporal cortex.

2.6.3 Signal detection

Electrical activity from the microelectrode was preamplified by a field effect transistor (NeuroLog head stage NL 100) and further amplified by a second preamplifier (NeuroLog NL 104). The neural signal (1-5KHz) was filtered (NeuroLog NL 125) below 0.5KHz and above 15KHz and displayed at slow time base (5ms/cm) on the main oscilloscope (Telequipment DM63). The activity of individual cells

was selected and digitized with a voltage window (Digitimer D.130).

When two or more cells were encountered with similar action potential amplitudes, the microelectrode position was adjusted until it was possible to discriminate one spike as having a larger amplitude than the other. The voltage trigger level could then be altered to catch only one of these spikes and using an analogue delay of 1ms (NeuroLog NL 740) the entire wave form of the selected action potential could be monitored on a second oscilloscope at fast time base (0.5ms/cm). Selected signals exceeding the lower voltage window level were also amplified for audio output through a loudspeaker system. This audio output enabled value judgements on the firing rate of a cell to be made and provided a good qualitative indication of neural responses to stimuli and an audible indication of electrode drift from a given cell.

2.6.4 Data analysis

a) On-line

Visual data: Stimuli were presented to the monkey behind a large aperture shutter (Compur Electronic 5FM 6.4cm aperture) which opened after a 0.5s signal tone (700Hz). The response magnitude was calculated as the total number of spikes occurring on each trial in the 250ms period starting 100ms after stimulus presentation. This period was used because all visual neurones studied responded with latencies of greater than 100ms and because closed circuit TV monitoring of the monkeys showed that attention to stimuli was

maintained for the first 500ms of presentation. [As eye movements were not usually recorded this closed circuit TV monitoring ensured that all stimuli were attended and fixated. On particular experiments where eye movements were recorded (with Ag AgCl electro-oculogram electrodes or with an infra-red corneal reflection system), the results confirmed stimulus fixation and tracking by the monkey and demonstrated that there was no direct connection between eye movements and the cell's firing pattern (see Appendix A).] Spontaneous activity was assessed in the 250ms before each trial onset. Data from the individual trials were analyzed on-line with a Cromemco System III microcomputer.

Tactile data: A Campden electronic "lickometer" was used to detect short current between the monkey and any conducting material used as a tactile stimulus. So, the onset or offset of tactile stimulation could initiate a trial such that the magnitude of cell response to the stimulus could be assessed, as before, for the visual data on a trial by trial basis. Since tactile cells often responded with a latency of less than 50ms, the response on each trial was measured as the total number of spikes occurring in the first 250ms period starting immediately after stimulus presentation (i.e. 0ms delay and not 100ms delay as for the visual data). During 'clinical' testing counts of the response rate (number of spikes in the first 500ms) were synchronized with the onset or offset of tactile stimulation and the mean response rate assessed over several trials of particular stimuli. 'Clinical' testing was favoured for the speed and ease with which data could be collected.

b) Off-line

For off-line analysis, a video recorder (JVC CR-6600E) with two auditory channels was used to simultaneously record the amplified electrical signal from the microelectrode, the signal tone (where appropriate) prior to stimulus presentation and vocal commentary. A colour video camera (Canon VC-20) was set up to film stimuli seen by the monkey so that cell activity could be compared to a particular dimension of the stimulus presentation. Analysis of the tapes was performed by replaying the neural recording signal through the main oscilloscope and measuring spike frequency at relevant periods during visual stimulation. (Measurement of spike frequency was performed using the latch counter of the DM630 spike processor externally gated for a period of 0.5s following the presentation of a stimulus.)

A computer program was written for the Cromemco System III in order that visual and tactile latencies may be assessed from post stimulus time histograms.

2.7 Histology and Cell Localization

Frontal and lateral X-radiographs (X-rays) were taken using a Portable X-Ray Apparatus (Type MX-2) at the termination of all the recording tracks (1-2s exposures at 16 KV). The X-ray apparatus was attached to the front and side of the primate chair at a fixed distance so that all the track X-rays were comparable. During the final weeks of recording, in order to locate the recording electrode's position,

small electrolytic lesions were made on particular tracks by applying a DC anodal current of 40-60 microamps for 30-60s.

At the end of the experiments, an animal was given a lethal dose of barbiturate anaesthetic, 2-3ml IP) and perfused with phosphate buffered saline and 10% formal saline. The brain was removed from the skull and after blocking, 1mm probes used stereotaxically to mark both hemispheres of the brain: (a) vertically - 10mm lateral to the midline at 4 intervals of 5mm anterior-posterior; and (b) horizontally - at 15mm lateral to the midline at 3 intervals of 10mm above zero (ear bar axis). The brain was then placed in a 4% solution of sucrose with 10% formalin, until it sank. This procedure was repeated with 10, 20 and 30% sucrose solutions. The brain was then cut on a cryostat microtome (5030, Bright Instruments Company Ltd, Huntingdon) into 25 micron sections. One section in every 0.25mm was mounted and stained with cresyl violet. The positions of the recording electrodes could then be determined.

From the X rays of each recording track the coordinates of the electrode tip, its depth and the gradient of the electrode track could be calculated and the recording positions of the cells graphically plotted at different anterior-posterior levels (in 1mm steps). Outline drawings of the histological sections were then constructed at the same magnification. With the X-ray photograph and histologically defined locations of the stereotaxic probes and micro-lesions, the X-ray reconstruction of the recording positions were correlated with the position of brain structures defined in the histological sections. The location of all cells recorded was reconstructed with an accuracy

of +/- 1mm.

2.8 References

Merrill, E.G., and Ainsworth, A. (1972) Glass coated platinum-plated tungsten microelectrodes. Med. biol. Eng. 10:662-672.

Snider, R.S., and Lee, J.C. (1961) A Stereotaxic atlas of the monkey brain (Macaca mulatta). Chicago University Press, Chicago.

CHAPTER 3

Somatosensory processing in the macaque neocortex: A review of relevant connectional, electrophysiological and ablation studies.

3.1 Introduction

In the following chapter a practical investigation of the electrophysiological properties of neurones in the superior temporal sulcus (STS) is described, with a view to placing the STS in recognized tactual processing pathways - a position not previously considered for the STS. To give this work appropriate perspective this chapter presents a comprehensive account of studies of those regions of the brain devoted wholly or partially to the processing of somatosensory information. These anatomical connection, electrophysiological and ablation studies have defined to date the essential characteristics of the tactual processing pathways upon which the following work is based.

A number of investigations have traced connections of primary and secondary somatic sensory areas with their association areas; and with the refinement and increased precision in neuroanatomical methods, in recent years, a more exact and detailed connectivity of these regions has been described. The adoption of single unit recording studies in awake, behaving animals has similarly opened up the field of electrophysiology, encouraging hypotheses on the correlation between

the properties of individual cortical neurones and certain behaviours. Consequently, the complex system of neural connections (interlinking the recognized cortical structures that advance somatosensory information within the cerebral cortex) can be identified, and some functional significance of these regions inferred from both ablation studies and investigations of the physiological properties of somatosensory neurones.

In order to trace the putative routes sensory information might take en route to the STS (important for considerations in Chapter 4), it becomes necessary to consider also the neural connections of those somatosensory areas which project to the STS; and the properties of cells in these areas which may input cells of the STS.

3.2 Somatosensory Neural Connections

To define divisions of the neocortex and their subdivisions, the different labelling systems of Brodmann (1905), Vogt and Vogt (1919, 1926) and von Bonin and Bailey (1947) are used.

The general pattern of connectivity for the primary and secondary somatic sensory areas and the posterior parietal association cortex (areas 5 and 7) with the STS and relevant subcortical structures (reviewed below) are summarized in Figure 3.1.

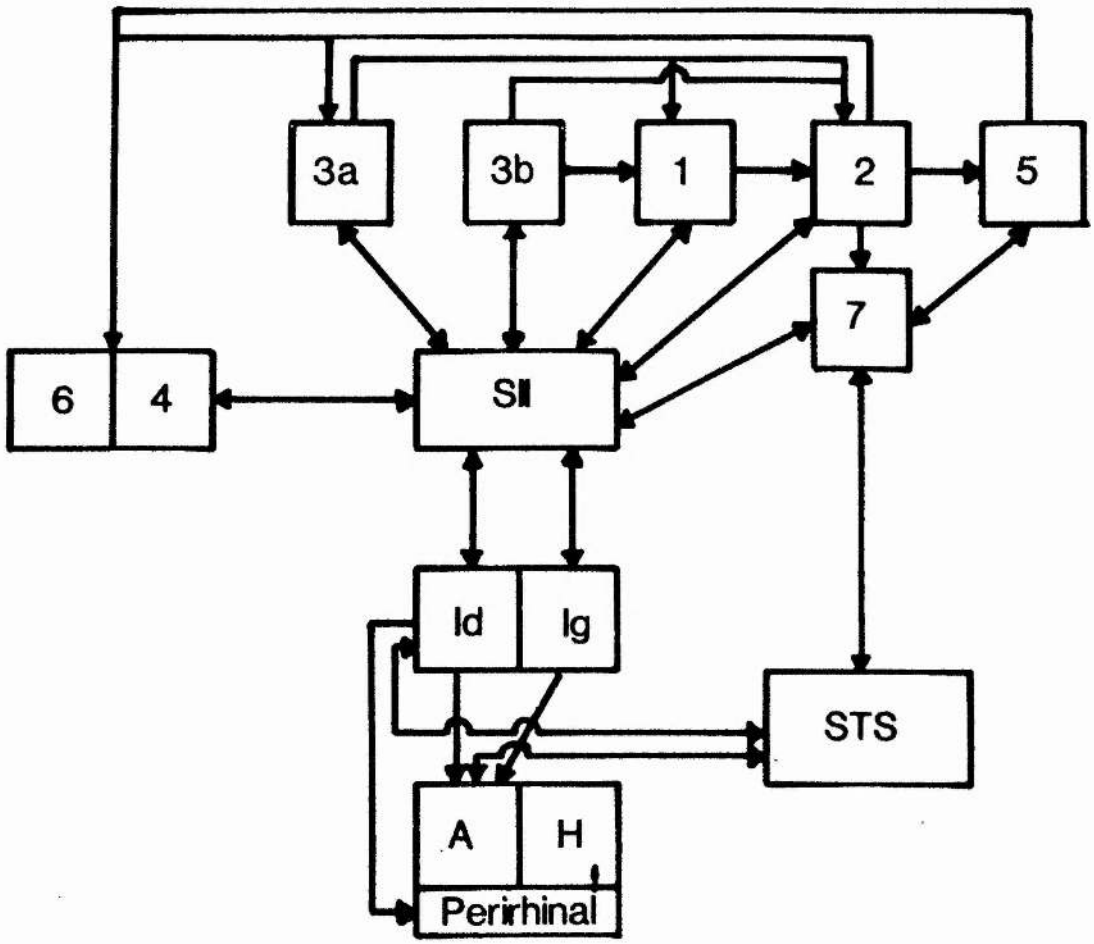


Figure 3.1 Summary of corticocortical and corticolimbic projections of the somatosensory fields, adapted from Friedman et al (1986) to include the superior temporal sulcus (STS). The STS is in a prime position to relay somatic information not just from SII (via the insular cortex, Id and Ig) to the amygdala (A) but also somato-spatial information from the posterior parietal cortex (5 and 7). H, hippocampus.

3.2.1 SI

The primary somatosensory cortex (SI) constitutes the first stage for somatosensory processing, and consists of Brodmann's (1907) architectural areas 3, 1 and 2 with area 3 subdivided by the Vogts (1926) into areas 3a and 3b. SI receives its predominant input from the ventrobasal region of the thalamus (Jones, 1983; Jones and Friedman, 1982); the thalamic input being strongest to area 3 rather than areas 1 and 2. Conversely, there is an increase in corticocortical projections (e.g. Bowker and Coulter, 1981) to these areas (1 and 2) as they receive inputs originating in areas 3a and 3b. Reciprocal projections exist between area 3a and areas 1 and 2. Area 2 also receives a direct projection from area 1 and primary motor cortex, area 4 (Bowker and Coulter, 1981). Unlike area 3b, areas 1 and 2 send axons to other cortical areas, anteriorly to motor areas 4 and 6 and posteriorly to area 5 (Bowker and Coulter, 1981; Jones et al, 1978; Vogt and Pandya, 1978). SI also reciprocates a projection with the second somatic sensory area, SII (Friedman, 1978; Friedman et al, 1980, 1982; Jones et al, 1978; Jones and Powell, 1969, 1970; Murray et al, 1980; Woolsey, 1958).

Friedman (1983) stressed a distinction between the 'forward' projection from SI to layers III and IV of SII and the 'backward' projection from SII to layer I of SI. He suggested a functional dichotomy where sensory information is transmitted through successive systems (areas 3, 1, 2 of SI and SII respectively) by the forward projections, and a modulatory influence exerted by the backward projections on the systems in which the projections originate.

Friedman (1983) proposed that the connectivity of all the sensory areas might be arranged in this way.

3.2.2 SII and insular cortex

The cortical connections of SII are described in some detail by Friedman et al (1982, 1986) who traced (with anterograde and retrograde axonal transport studies) the connectivity of SII with the insular, retroinsular (Ri) cortex and the posterior parietal cortex. Connections have been confirmed between SII and areas 3a, 3b, 1 and 2 and between area 5 and both area 7 and Ri. SII is reciprocally connected with the retroinsular area, area 7b and the granular (Ig) and dysgranular (Id) insular fields (defined by Roberts and Akert, 1963).

Friedman et al (1986) have demonstrated a reciprocal connection between the dysgranular insula and the upper and lower banks of the STS. Subcortically, the insular cortex projects to the amygdaloid complex (Aggleton et al, 1980; Friedman et al, 1986; Mufson et al, 1981) and it is interesting to note that Aggleton et al (1980) demonstrated that the STS projects to the same nucleus of the amygdala as the insula, the basolateral nucleus. Id projects, in addition, to the perirhinal cortex which supplies input to the hippocampal formation.

3.2.3 Posterior parietal association cortex

Both the primary (SI) and the secondary (SII) somatic sensory areas project to the posterior parietal association cortex which in turn projects to the STS, hence the intracortical and corticocortical connections of areas 5 and 7 bear distinct significance to this treatise. Consequently a descriptive account of the connectivity framework of the parietal cortex is given below. For the interested reader Pandya and Yeterian (1985) give an account of the architecture and connections of the somatosensory association areas and Hyvarinen (1982) a general review of the neural connections of the posterior parietal lobe in monkeys.

Intracortical connections of the superior and inferior parietal lobes described by Pandya and Yeterian (1985) appear to follow a systematic rostro-caudal progression. Input from the dorsal half of area 2 of SI projects to PEc, the upper bank of the intraparietal sulcus (PEa) and an area on the medial surface of the superior parietal lobe, PGm. These areas (PE, PEc, PEa and also PEci) project back to PFop which corresponds in part with SII defined by Woolsey (1958). PGm projects to the upper bank (PEa) and the fundus (IPd) of the intraparietal sulcus, in addition to an area of the inferior parietal lobe, PG. Input from ventral area 2 of SI projects to PF (area 7b in the inferior parietal lobe) which is connected to both PFG and PG (area 7a). PFG also projects to PG and both PF and PFG are connected to the lower bank of the intraparietal sulcus, POa, and PGop.

In the same way that PGm projects to the upper bank and fundus of the intraparietal sulcus (IPS), so PG projects to the lower bank (POa) and fundus of the IPS and also to PGm. Thus, PG and PGm have similar

patterns of connectivity and are interconnected.

SI and SII are closely associated with the superior (PE) and the inferior (PF) parietal lobes rostrally, but caudally PG and PGm are only indirectly related to the primary and secondary somatic areas (Pandya and Yeterian, 1985). This differential connectivity is consistent with the suggestion that rostral parietal association areas are involved in more basic somatosensory processing while caudal areas may subserve more complex functions (Hyvarinen, 1982) described in section 6.3. Seltzer and Pandya (1984) propose that PE and PF are receiving a topographically organized somatic sensory cortical input while PG receives convergent somatic sensory and visual input, that is PG is not modality specific.

Seltzer and Pandya (1984) reported no projection from the superior parietal lobule or upper bank of the IPS (areas PE and PEa) to the STS although a projection from the apex of the superior parietal lobe (PEc) and the medial surface of the parietal lobe (area PGm) to areas TPO and PGa in the upper bank of the STS were observed. Similarly, no projections from the rostral third of the inferior parietal lobe (area PF and rostral area PFG) to the STS were noted, but projections from the middle and caudal thirds of the inferior parietal lobe (caudal PFG, PG and Opt) to the upper bank of the STS (areas TPO and PGa), and the lower bank of the IPS (POa) to the rostral depth (area IPa) of the STS were observed.

To summarize, a discrete region in the caudal third of the inferior parietal lobe, corresponding to Pandya and Seltzer's (1982) area PG

and area Opt, gives rise to the majority of parietal projections to the STS. Other posterior parietal regions send only modest projections to the STS. In this context, the parieto-temporal connections may be thought of as two types: (1) projections emanating from the modality-specific zones, e.g. mid-inferior parietal lobe, lower lip of IPS and cortex in medial surface of parietal lobe, which may convey somatic sensory information to the STS (Seltzer and Pandya, 1984); and (2) projections originating in the caudal inferior parietal lobe which may convey highly complex non-modality-specific information, possibly spatial in nature (Ungerleider and Mishkin, 1982).

3.2.4 Superior temporal sulcus (STS)

That the STS receives projections from the posterior parietal lobe is not in dispute. Connections between the posterior parietal cortex and the STS have been demonstrated by a number of authors (e.g. Chavis and Pandya, 1976; Jones and Burton, 1976; Jones and Powell, 1969, 1970; Mesulam et al, 1977; Pandya and Kuypers, 1969; Pandya and Seltzer, 1982; Seltzer and Pandya, 1978). However, the type of information being projected to the STS, i.e. modality specific (visual or somaesthetic) or crossmodal, is still unspecified.

Other afferent cortical projections to the STS emanate from the superior temporal gyrus, the inferior temporal cortex (ITC) and striate cortex (Gross et al, 1981; Jones and Burton, 1976; Mesulam et al, 1977; Seltzer and Pandya, 1978) and the insular cortex (Friedman

et al, 1986). Five regions of the ITC project predominantly to the caudal lower bank of the STS, area TEa, with a modest projection to IPa (Seltzer and Pandya, 1978). Areas 17 and 19 of the visual cortex project to area OAa in the rostral region of the floor of the STS and area 19 projects also to areas TPO and PGa in the STS. Polysensory areas including the amygdala, cingulate gyrus, parahippocampal region, frontal eye fields and medial pulvinar also extend projections to the STS (e.g. Aggleton et al, 1980; Jones and Burton, 1976; Jacobsen and Trojanowski, 1977).

The STS sends diffuse efferents to the amygdala, cingulate gyrus, parahippocampal gyrus, posterior parietal cortex (PG) and the frontal cortex (Aggleton et al, 1980; Jacobsen and Trojanowski, 1977; Jones and Powell, 1969, 1970a,b; Mesulam et al, 1977).

It was Jones and Powell (1970a) who first suggested that information from all three modalities came together in the depths (fundus) of the STS and with this wide afferent input to the STS a crossmodal convergence of sensory modalities is certainly possible.

A review of these elaborate connectional systems has been considered independently from the following review of the physiological and functional properties of these areas, but this should not encourage a separate view of the two sections. They are intimately associated and separated only to simplify and clarify the work presented.

3.3 Physiological Properties of Somatosensory Neurones

Mishkin (1979), Murray et al (1980) and Murray and Mishkin (1984) have proposed a cortical pathway for somatosensory processing in monkeys. They suggest that information in this tactile processing pathway proceeds from the primary somatosensory cortex (SI) to certain limbic structures of the temporal lobe through progressive links in SII and the insular cortex. A parallel is drawn between this cortico-limbic system for touch (SI-SII-insular cortex-limbic structures) and the cortico-limbic route for vision (striate-prestriate-inferior temporal cortex-limbic structures). Murray and Mishkin (1984) suggest that this cortico-limbic route for tactile information was responsible for the ability to discriminate and recognize objects by touch in much the same way as the route for vision via the temporal cortex (including the STS) is thought to serve visual discrimination and recognition abilities (e.g. Gross et al, 1981; Mishkin, 1966; Ungerleider and Mishkin, 1982).

Murray and Mishkin (1984) suggest that SII, but <u>not</u> area 5, is critical for tactile discrimination. Area 5 may play an essential role in another (parallel) tactile processing pathway considered to be specialized for 'active touch' (Werner and Whitsel, 1973) where information proceeds from SI to area 5 to area 7 and the cingulate cortex (Friedman et al, 1982, 1986; Mufson et al, 1981) to the limbic structures of the temporal lobe. Friedman et al (1982, 1986) noted that this latter set of connections could serve a hierarchically organized cortico-limbic pathway for tactile spatial perception. The position of the STS (if it has one) in such pathways is unknown, yet the connection studies intimate a final cortical stage in sensory processing for the STS. However, it is only with knowledge of the

type of information the STS receives, and the physiological properties of somatosensory cells in the STS itself, that will allow verification of this. So, each pathway will be discussed separately in terms of the physiological properties of the cells constituting each of the somatosensory processing areas (comprising the tactile pathways), and some functional implications made from this.

3.3.1 The SI-SII-insular cortex pathway

(a) SI

Classically SI was described as a single and largely continuous representation of the body surface spanning the four distinct architectonic regions 3a, 3b, 1 and 2 anteriorly to posteriorly (Jones and Powell, 1969, 1970 a,b; Powell and Mountcastle, 1959 a,b; Woolsey, 1958). More recent studies have revealed two complete representations of the superficial body surface and structures within SI, coincident with cytoarchitectonic areas 3b and 1 (Kaas et al, 1979, 1981; Merzenich et al, 1978, 1981; Paul et al, 1975) and two representations of deeper body tissues in areas 3a and 2. Iwamura et al (1981) dispute an independent representation of body parts in the posterior part of SI (area 2) and instead propose that this region associates or integrates complex somatosensory information from several areas across several submodalities. Without further clarifying these independent body maps it is difficult to establish which view is correct. Merzenich et al (1981), however, did stress that these body representations could not be accurately depicted by a continuous body figure or 'homunculus'.

The receptive field size and the complexity of the functional properties of the neurones has been observed to increase posteriorly, through the cytoarchitectural subdivisions of the postcentral gyrus, from area 3a to 3b, to areas 1 and 2 (Hyvarinen and Poranen, 1978b; Iwamura and Tanaka, 1978 a,b,c; Iwamura et al, 1985 a,b). Hyvarinen and Poranen (1978b) categorized the receptive fields in SI into three groups: Small (one finger or one palmar whorl on the skin), medium (2-3 fingers on one hand, or an area of half the palm) and large (several fingers, the whole palm or an even larger area). They observed that the percentage of small receptive fields decreased and the large receptive fields increased progressively from area 3b to areas 1 and 2.

In parallel with this increase in receptive field size, the convergence onto single neurones of information from different somaesthetic submodalities is more common in the posterior part of the gyrus (Hyvarinen and Poranen, 1978 a,b). In area 3a most neurones were activated by joint or muscle manipulation, while in area 3b the majority were driven by light contact to the skin and hairs (Hyvarinen and Poranen, 1978 a,b; Iwamura et al, 1981; Powell and Mountcastle, 1959 a,b). In areas 1 and 2 neurones exhibited submodality convergence such that skin and hair or skin and joint manipulation units were found. The occurrence of movement sensitive and direction and orientation-selective (complex) cutaneous neurones increased from anterior to posterior within the postcentral gyrus; with the majority of these neurones being found in area 2 (Constanzo and Gardner, 1980; Hyvarinen, 1982; Hyvarinen and Poranen, 1978 a,b; Iwamura et al, 1981; Mountcastle et al, 1969; Schwarz and Fredrickson, 1971; Whitsel et al,

1972). A number of units were activated only at the moment of voluntary movements or by specific modes of stimuli and these were also more commonly found in area 2 (Iwamura et al, 1981; Sakata and Iwamura, 1978).

Receptive field integration in SI (more specifically areas 1 and 2) is thought to be useful for discriminating different types of contact of the body to the surroundings (Sakata and Iwamura, 1978). As such it would provide essential information for discriminating between objects of differing size, texture or weight in the tactile modality. The convergence of different submodalities (Iwamura et al, 1981; Sakata and Iwamura, 1978) and the prevalence of neurones in area 2 sensitive to the edges of objects passing across cutaneous receptive fields (Iwamura et al, 1982) indicate the presence in SI of systematic mechanisms for feature extraction and the discrimination of objects grasped by the hand.

The changes that take place in the functional properties of cells when moving across these different cytoarchitectural areas in SI suggest a degree of intracortical information processing (coding larger body regions and more complex combinations of information) within the posterior part of the postcentral gyrus (Hyvarinen and Poranen, 1978 a,b).

(b) SII

The next stage in this cortico-limbic tactile pathway is the second somatosensory cortex (SII) which occupies the superior bank of the sylvian fissure, posterior to the level of the central sulcus. The

topographic organization of SII has been extensively examined and a representation of the whole body surface has been mapped (Burton and Robinson, 1981; Friedman, 1981; Juliano et al, 1983; Whitsel et al, 1969); this representation is limited to the cutaneous body surface (Whitsel et al, 1969). Burton and Robinson (1981) illustrate clearly the somatotopic organization of SII. Briefly, the map of the body is organized in anterolateral to posteromedial slanted strips that align in an anterior to posterior sequence across the parietal operculum (Burton and Robinson, 1981; Friedman, 1981; Whitsel et al, 1969) with the face, jaw, neck, chest, preaxial forelimbs and palmar aspects of the hands represented sequentially in a medial to lateral direction (Whitsel et al, 1969).

A clear delineation of SII into two portions has been reported (Burton and Jones, 1976; Poranen and Hyvarinen, 1982; Whitsel et al, 1969). These regions have been described as: (1) a caudal portion extending several millimetres posterior to the interaural plane, and (2) a rostral portion (termed SIIr) extending anteriorly to the level of the central sulcus (Whitsel et al, 1969). The receptive fields and sensory properties of the neurones in these two anatomically segregated regions of SII are not identical. The caudal portion of SII consists of neurones with wide, cutaneous, often discontinuous and asymmetrical receptive fields (Burton and Jones, 1976; Burton and Robinson, 1981; Poranen and Hyvarinen, 1982; Whitsel et al, 1969). Notably, a large number of contralateral receptive fields were observed in this region of SII (Burton and Robinson, 1981; Poranen and Hyvarinen, 1982).

In contrast, in the rostral (or anterior) portion of SII two types of receptive fields were encountered: Large bilateral receptive fields continuing across the body midline; and smaller, disjointed receptive fields positioned toward the apices of the extremities (Burton and Jones, 1976; Burton and Robinson, 1981; Poranen and Hyvarinen, 1982; Whitsel et al, 1969). The large receptive fields cover both arms, shoulders, chest and back, or the legs and the lower half of the body i.e. the upper and lower torsos (Poranen and Hyvarinen, 1982; Whitsel et al, 1969). Interestingly the body midline appears in the topographic map four times, each time in the context of a different body region (Whitsel et al, 1969).

Similarly, a dichotomy between the sensory properties of the neurones in the rostral and caudal regions of SII has been noted. The caudal (posterior) portion of SII consists of neurones sensitive at a high stimulus threshold to heavy pressing or squeezing, i.e. nociceptive mechanical stimuli (Burton and Jones, 1976; Whitsel et al, 1969). In direct contrast, neurones in the rostral (anterior) portion of SII respond to gentle tactile stimuli, i.e. the onset or offset of light cutaneous stimulation (Burton and Jones, 1976; Friedman, 1981; Poranen and Hyvarinen, 1982; Whitsel et al, 1969), with only few cells responding to deep touch. For the majority of these cells a movement of the stimulus (in any direction) across the receptive field elicited a greater response than a static stimulus (Friedman, 1981; Whitsel et al, 1969).

(c) Insular cortex

The insular cortex (buried in the depths of the lateral sulcus) is

postulated as the final component in the somatosensory link to the limbic system (Murray and Mishkin, 1984; Murray et al, 1980). Little electrophysiological investigation of this area of cortex has been made; indeed Robinson and Burton (1980a) stated of their own work that their sample of neurones was too small to permit any extensive comment. However, of the few studies that have been made, all the results seem to be in accordance. There is no topographical organization of the body in the insular cortex; the receptive fields are large (upper or lower torso, or the whole body); and the majority of neurones in the insula respond to passive, innocuous (non-nociceptive) somatic stimuli, although occasionally active movement by the monkey is necessary to obtain a response (Burton and Robinson, 1981; Juliano et al, 1983; Robinson and Burton, 1980 a,b). Robinson and Burton (1980a) have reported a few cells in the granular insular cortex with multimodal properties.

3.3.2 The SI-area 5-area 7 pathway

(a) Area 5

The primary somatic sensory cortex (and SII) projects information to the posterior parietal association cortex which comprises the superior and inferior lobes. Considering first the superior parietal lobe (area 5, Brodmann (1905); PE, von Bonin and Bailey (1947)), some topographical order is recognized although overlapping of somatotopical subdivisions has been reported within the gross organization (Sakata, 1975; Sakata and Iwamura, 1978). Medially, the hindlimb is represented, then the trunk, the shoulder and the upper

arm laterally, with a hindlimb-forelimb overlap between these two regions (Sakata, 1975).

Evidence for topographic convergence is also supported by an increase in the size of the receptive fields of neurones in area 5. Receptive field organization is strikingly different to that in SI. The receptive fields are larger and not necessarily restricted to the contralateral side of the body; ipsilateral but more commonly bilateral receptive fields have been additionally identified (Duffy and Burchfield, 1971; Mountcastle et al, 1975; Sakata, 1975; Sakata et al, 1973). Cutaneous receptive fields often covered one whole extremity or both halves of the chest or abdomen (Mountcastle et al, 1975; Sakata et al, 1973). In general joint receptive fields were more difficult to define.

Mountcastle et al (1975) reported that the majority of neurones they observed had a receptive field covering a single joint, with only 10% of the cells including two or more joints. Other groups of workers have however claimed that more neurones have receptive fields covering two or more joints (Duffy and Burchfield, 1971; Sakata, 1975; Sakata et al, 1973). It is easy to see how this discrepancy could occur when considering the sensory properties of these cells, as the 'best' stimulus for many of these neurones is the simultaneous stimulation of several joints or joints and cutaneous receptive fields. These receptive field properties and combinations would be difficult to fully investigate passively with awake, behaving monkeys. Indeed, three main classes of neurones have been identified with one class related to joints or position sense, a second related to the skin or

touch, and the third related to both skin and joints or touch and position sense (Duffy and Burchfield, 1971; Mountcastle et al, 1975; Sakata, 1975; Sakata et al, 1973). Area 5 is closely associated with SI as far as these submodalities are concerned although submodality convergence is more common in area 5 than in SI where the submodalities tend to be segregated (Sakata and Iwamura, 1978; Sakata et al, 1973).

Many of the complex stimuli that are optimal for single neurones correspond to combinations of joint positions and movements assumed during natural poses occurring frequently as a part of the monkey's normal behaviour (Duffy and Burchfield, 1971; Sakata et al, 1973). Notably, kinaesthetic input is more dominant in area 5 than cutaneous input (Duffy and Burchfield, 1971; Hyvarinen, 1982; Mountcastle et al, 1975; Sakata, 1975; Sakata et al, 1973). The neurones that were activated by cutaneous stimulation did not show any striking differences from those in SI. Many of these cells preferred a moving stimulus to static stimulation (Mountcastle et al, 1975; Sakata et al, 1973) and a large proportion of these neurones were directionally selective.

Sakata et al (1973) proposed that the joint combination units might be regarded as some stage of a 'recoding' process between a level at which separate information of the position of individual joints is represented and that at which the spatial position of a segment of the body is presented. This would seem to be a necessary step for the holistic concept of the body image (Sakata and Iwamura, 1978; Sakata et al, 1973). Joint and skin neurones may play an essential role in

the process for the extraction of 3-dimensional features of an object and some neurones of this type may give rise to the neural code of the spatial position of the tactile object relative to the body axis (Sakata, 1975; Sakata et al, 1973). Sakata et al (1973) suggested that 'matching' neurones may represent certain aspects of the body form more completely than joint combination neurones (the position of one body part in reference to other body parts) or they may be related to certain features of external objects held between two parts of the body. Information from both the 'matching' neurones and cutaneous neurones may also enable area 5 to be involved in the analysis of the location of a cutaneous receptive field in reference to the body axis.

In addition to the various types of somatosensory neurones, a small proportion of cells were found that were not activated by any form of passive stimulation, but rather, were responsive during active exploratory movements of the hands and arms (Hyvarinen and Poranen, 1974; Mountcastle et al, 1975). (A considerably greater number of this type of cell were observed in area 7.) Mountcastle et al (1975) described two groups of this type of neurone: Projection neurones related to manual reaching, i.e. projection of the monkey's arm towards an object in the monkey's extrapersonal space; and hand-manipulation neurones related to the monkey's active manipulation of an object within its extrapersonal space. They suggested that these neurones may be command cells controlling signals for exploratory movement.

It was found occasionally that some neurones in area 5 could be activated by visual as well as somatosensory stimulation (Mountcastle

et al, 1975; Sakata, 1975; Sakata et al, 1973). For these neurones similar directional preferences were observed in both sensory modalities, for example a cell sensitive to stroking downward in a lateral to medial direction on the contralateral neck also preferred a visual stimulus moving down (as opposed to up) in front of the monkey's face. The somaesthetic response was always dominant; the response to the visual stimulus being somewhat unstable (Sakata, 1975; Sakata et al, 1973). Sakata et al (1973) thought it possible that the somaesthetic information of the spatial position of an object represented at the single cell level was directly correlated with visual information concerning the spatial position of the object within the monkey's immediate extrapersonal space.

The convergence of information from other somatosensory areas onto area 5 and the convergence partially within area 5 itself is organized in such a way as to make units sensitive to particular patterns of stimuli (Sakata, 1975; Sakata et al, 1973). The combination of the visual and somaesthetic information from the area 5 neurones may be essential for the perception of posture and the movement of the body as well as aiding sensory guidance of purposeful motor acts (Hyvarinen, 1982; Leinonen, 1984; Sakata, 1975; Sakata et al, 1973). Area 5 could therefore play a role in space perception through the somaesthetic modality (Hyvarinen, 1982; Leinonen, 1984; Sakata, 1975).

(b) Area 7

The inferior parietal lobe (area 7) has been widely investigated (Hyvarinen, 1981; Hyvarinen and Poranen, 1974; Leinonen, 1980; Leinonen et al, 1979; Leinonen et al, 1980; Leinonen and Nyman, 1979;

Lynch et al, 1977; Mountcastle et al, 1975; Robinson and Burton, 1980a,b) and studies suggest that within area 7 there are functionally different regions. What have appeared to be incompatible results from these studies are likely accounted for in part by the differences in the locations of investigators' recordings within area 7. An attempt is made to clarify the physiological and functional properties of these regions and of area 7 as a whole.

A crude somatotopy, representative of major portions of the body, is demonstrated in associative area 7 (Hyvarinen, 1981; Robinson and Burton, 1980 a,b) such that the face is represented most laterally, the body and legs most medially with large overlapping regions (Hyvarinen, 1981). The cutaneous representation of various body parts coincides with the representation of active touch and movement by the same body parts across area 7; but a kinaesthetic region in the posterior part of area 7a did not exhibit this somatotopy (Hyvarinen, 1981).

Anterolaterally a region of area 7 (close to the lateral tip of the intraparietal sulcus) was described by Leinonen and Nyman (1979) as an 'associative face area'. Here, two-thirds of the cells responded to somatosensory and/or visual stimulation and one third to the monkey's own movements. The somatosensory receptive fields of these cells were larger than those in the surrounding face region of area 2 (Schwarz and Fredrickson, 1971), covering the lower jaw, nose, anterior neck, shoulder or lower arm. The cutaneous cells were responsive to light touching of the skin or palpation or passive stretching of the facial muscles.

The neurones responding to both somatosensory and visual stimulation were activated by light touching of the skin and a visual stimulus approaching the cutaneous receptive field or held near it. Even when the cutaneous receptive field could not be seen by the monkey only stimuli approaching the receptive field evoked a response implying that the direction of movement was in reference to the relative position of the cutaneous receptive field sensed through the somaesthetic modality rather than the location of the projection of the referred skin on the retina.

Complex somatic properties were exhibited by cells active when the monkey brought an object to its mouth by hand, when reaching for an object with its lips, or while chewing. So the cellular activity in the anterolateral part of area 7 is prominently related to the stimulation or motor activity of the face or mouth (Hyvarinen, 1981; Leinonen and Nyman, 1979) and it is suggested that these cells participate in the intercoordination of spatial information sensed through different sensory modalities (visual, exteroceptive, proprioceptive) and that the representation of the face within the somatosensory system is used as a reference for all stimuli moving with respect to one of these spatial modalities (Leinonen and Nyman, 1979).

Area 7b: Studies of the lateral region of the inferior parietal lobe, termed 7b (Vogt and Vogt, 1919) or PF (von Bonin and Bailey, 1947) have revealed the cells' properties in this region to be more reminiscent of those in SII than of those in area 5a (Leinonen et al, 1979; Robinson and Burton, 1980a,b). Most cells investigated in the

lateral part of area 7 responded to cutaneous, proprioceptive or visual stimulation (Leinonen et al, 1979; Robinson and Burton, 1980a,b).

Somatosensory receptive fields varied but were usually large ranging from the tips of digits (Robinson and Burton, 1980a) to entire parts of the body e.g. hand, arm, shoulder, chest (Leinonen et al, 1979; Robinson and Burton, 1980a); visual receptive fields often included both halves of the visual field (Leinonen et al, 1979; Robinson and Burton, 1980a). The cutaneous neurones usually responsive to light touching of the skin were often directionally selective, and for cells with receptive fields of the upper trunk the effective direction was towards the head, and on the head - towards the mouth (Leinonen et al, 1979).

Some cells in area 7b could be activated by either visual (less than 20%) or visual and somatosensory stimulation (Leinonen et al, 1979; Robinson and Burton, 1980b). A large proportion of the visual cells responded to moving stimuli, some with directional selectivity to objects moving either toward or away from the monkey, to its left or right, up or down. A few cells were responsive to 'interesting' stimuli such as food or novel objects (Leinonen et al, 1979).

For cells responding to both somatosensory and visual stimulation the cutaneous receptive fields covered the arms, chest, arm and chest or chest and face and these cells were active to light touching of the skin and to visual stimuli moving towards the cutaneous receptive field, in the same way as the cells in Leinonen and Nyman's (1979)

'associative face area' (Hyvarinen et al, 1975; Leinonen et al, 1979; Sakata et al, 1977).

Cells discharging only during active movements of the limbs included cell types responsive to reaching with the hand, manipulation of objects, and grasping and bringing an object to the mouth (Leinonen et al, 1979; Robinson and Burton, 1980a). Leinonen et al (1979) concluded that the lateral part of area 7 participates in intersensory analysis of spatial relations between moving stimuli and the monkey's own movements and suggested that this area is specialized in the spatial control of arm movements. Goldberg and Robinson (1977) proposed a possible role for area 7b in relating somatic sensory events with the behavioural significance of the stimulus.

Area 7a: Investigations perpetrated more medially to those mentioned above have identified a more posterior part of area 7 termed 7a (Vogt and Vogt, 1919) or PG (von Bonin and Bailey, 1947) predominantly concerned with somatic, visual and eye-movement signals (Hyvarinen, 1981; Hyvarinen and Poranen, 1974; Leinonen, 1980; Lynch et al, 1977; Mountcastle et al, 1975; Robinson et al, 1978; Yin and Mountcastle, 1977). One third of the neurones in area 7a are responsive to manual explorations of the monkey's extrapersonal space by manual reaching or arm projection, manual tracking and hand manipulation (Hyvarinen and Poranen, 1974; Leinonen, 1980; Mountcastle et al, 1975). The response properties of these cells are identical to those described in area 5.

Over half of the cells respond to visual exploration of the monkey's extrapersonal space and these neurones have been commonly defined as:

(1) visual fixation or looking neurones responsive when the eyes are focused on a specific location of a stimulus in the visual field; (2) visual tracking neurones responsive during smooth pursuit of an object of interest (within arm's reach) moving through the visual field; and (3) visual space neurones responsive to stimuli presented peripherally (Hyvarinen and Poranen, 1974; Leinonen, 1980; Lynch et al, 1977; Mountcastle et al, 1975). Lynch et al (1977) also described saccade neurones which were activated just prior to the eye's saccadic movement and incidentally reported 80% of cells (in a study of a medial region of area 7a) exclusively responsive to eye movements. Mountcastle et al (1975) and Lynch et al (1977) have claimed that the responses of the visual fixation, tracking and saccade cells are dependent on attentional and motivational factors .

A few cells in area 7a have been reported responsive to cutaneous stimuli (both light and deep touch) but these were rare (Hyvarinen and Poranen, 1974; Leinonen 1980). Mountcastle et al (1975) reported 2% of cells sensitive to passive stimulation of joints. The wide receptive fields of these cells were identical to those of similar cell types in area 7b.

In addition to these pure-modality responses, convergent neurones have been described (Hyvarinen and Poranen, 1974; Mountcastle et al, 1975) that are activated by visual fixation and arm projection (looking and reaching neurones) for hand-eye coordination, and cutaneous stimulation and visual fixation (touch and looking neurones) for detection of movement near the cutaneous receptive field. In area 7a there is, therefore, a convergence of motor, visual and oculomotor

signals for the control of eye and limb movements.

That a number of functions have been assigned to area 7a is of no surprise considering the variety of cell types in this region of cortex. Neurones coding eye movements may participate in monitoring the visual field for interesting stimuli i.e. directing visual attention (Lynch et al, 1977; Robinson et al, 1978) and in combination with active limb movements may effect spatial guidance, i.e. enable the monkey to direct fine movements performed under visual guidance and make postural adjustments (Hyvarinen, 1982; Hyvarinen and Poranen, 1974).

Sensorimotor interaction may provide a somatosensory coordinate system (or sensory basis) for spatial perception or goal-directed voluntary movements (Hyvarinen, 1982; Hyvarinen and Poranen, 1974; Mountcastle et al, 1975). In terms of a spatial schema the analysis of an object's location and distance (and direction of an object moving) with reference to the body, i.e. a spatial representation of the body and environment (the monkey's immediate extrapersonal space) may guide motor acts to targets of interest (Hyvarinen, 1982; Hyvarinen and Poranen, 1974; Leinonen, 1980; Sakata et al, 1978, 1980). Mountcastle et al (1975) suggested that the movement-related sets of neurones may actually control or command arm and eye movements and so function as a command apparatus for behavioural acts of the monkey and the visual exploration of the monkey's extrapersonal space.

3.3.3 The Superior Temporal Sulcus

Suffice to say there have been no primarily somatosensory investigations of neuronal properties in the STS. Bruce et al (1981) give a superficial account of somaesthetic response properties indicating only the general nature of these cells, i.e. 'almost always large ... receptive fields', and 'usually any type of stimuli ... would elicit a response'. This work is discussed in greater detail in the next chapter (4) in terms of the findings presented there.

3.4 Somatosensory Ablation Studies

3.4.1 SI

Randolph and Semmes (1974) showed that selective ablation of the three cytoarchitectural areas of SI led to differential deficits in somaesthetic tasks. Ablation of area 3 impaired performance on all somatosensory discrimination tasks, whereas removing area 1 resulted in deficits in discrimination of texture and the ablation of area 2 in deficits in discrimination of angles.

3.4.2 SII

Investigations of tactile discrimination by monkeys after ablations of SII have reported severe deficits (Murray and Mishkin, 1984; Murray et al, 1980; Ridley and Ettlinger, 1976, 1978) in performance on

discrimination tasks. Murray and Mishkin (1984) reported that monkeys with SII ablated were impaired on both texture and shape discrimination learning and that their size and surface roughness discrimination thresholds were elevated. A role in tactile discrimination and learning has therefore been postulated for SII (Friedman, 1981; Murray and Mishkin, 1984; Murray et al, 1980).

3.4.3 Insular cortex

Monkeys with an ablation of the insular cortex have been shown to be impaired on tactile discrimination tasks (other than size or roughness - Murray et al, 1980) which implies that the insula does play an integral part in the tactile recognition and memory processing pathway although some of its functions remain elusive.

3.4.4 Area 5

The defects produced in monkeys by ablation of the entire posterior parietal cortex (areas 5 and 7) include the impairment of visuo-spatial orientation. Monkeys were deficient in route finding tasks (Bates and Ettlinger, 1960; Petrides and Iverson, 1979; Sugishita et al, 1978), showed a disorder in reaching for objects (e.g. Hartje and Ettlinger, 1973) and misdirected manual searching in the dark (Ratcliff et al, 1977). Pohl (1973) and Ungerleider and Brody (1977) found that parietal lesions disturbed the monkey's ability to perceive spatial relations between objects and Milner et al

(1977) suggest that sensori-motor coordination rather than simply spatial perception is disturbed. Although these studies were not directed to particular cytoarchitectonic areas within the parietal cortex, many of the deficits described related to the sensori-motor functions of area 5 suggested from electrophysiological studies. The specific ablation of area 5 by Peele (1944) and the cooling techniques adopted by Stein (1976, 1978) indicate that area 5 contains mechanisms necessary for the somaesthetic control of reaching.

Somaesthetic discrimination deficits may also be produced by posterior parietal lesions, e.g. difficulties in roughness discrimination (Murray and Mishkin, 1984; Semmes and Turner, 1977; Stein, 1978). Separate ablation of area 5 did not impair tactile discrimination (Murray and Mishkin, 1984; Semmes and Turner, 1977) so although somaesthetic deficits may be produced by lesions in area 5 this area does not appear to play an exclusive role in somatosensory discrimination (Murray and Mishkin, 1984; Semmes and Turner, 1977). This function has already been suggested for SII in the first pathway.

3.4.5 Area 7

The effects of general posterior parietal cortex lesions have been discussed earlier but it is helpful to re-emphasize some results of these studies. With lesions of the posterior parietal cortex sensorimotor coordination is disturbed (Milner et al, 1977) and deficits are found in visually guided somatomotor tasks (Petrides and Iverson, 1979) and in visual search (Latto, 1978). After lesions

limited to the cytoarchitectural region of area 7 Peele (1944) observed that the monkey's contralateral hand groped for targets and was ataxic. Ablation of area 7b resulted in an impairment in both tactile and visual placing and grasping (Fleming and Crosby, 1955). Stein (1978) observed slowing of eye movements and the neglect of the contralateral visual half-field with the cooling of area 7 and concluded that area 7 contains mechanisms for the visual control of reaching accuracy in contrast to somaesthetic control in area 5. Ablation studies in the monkey suggest that area 7 participates in the localization of stimuli in different sensory systems and the guidance of movements with the aid of visual and somaesthetic stimuli (Leinonen, 1981). The intersensory associations required for such behaviours are revealed at the cellular level.

3.4.6 STS

These deficits, resulting from the ablation of certain areas of somatosensory neocortex, help us to see where these areas of the brain fit into a general schema of tactile processing for recognition, discrimination, learning and memory. An obvious question is, therefore: Do selective impairments of the STS go anyway towards revealing a tactual function for this area? The current literature cannot adequately answer this question as specific tactile tasks have not readily been incorporated into STS ablation studies. No impairments have been reported on tactual to visual cross-modal matching or visual-tactile cross-modal recognition (Ettlinger and Garcha, 1980). The only positive report on any form of tactile

deficit is given by Luh et al (1986) who report severe trimodal neglect with a bilateral STS lesion. It is perhaps a tautological argument to infer that physiological evidence of single neurone function in the STS may be necessary for 'appropriate' tasks to be designed on which impairments could be reflected. What seems clear is the need for further study on all aspects of tactile processing within the STS.

3.5 References

Aggleton, J.P., Burton, M.J., and Passingham, R.E. (1980) Cortical and subcortical afferents to the amygdala of the rhesus monkey (Macaca mulatta). Brain Res. 190:347-368.

Bates, J.A.V., and Ettlinger, G. (1960) Posterior biparietal ablations in the monkey. Arch. Neurol. 3:177-192.

Bowker, R.M., and Coulter, J.D. (1981) Intracortical connectivities of somatic sensory and motor areas: multiple cortical pathways in monkeys. In: C.N. Woolsey (ed.) Cortical Sensory Organization, Volume 1, Multiple Somatic Areas. Humana Press, Clifton, N.J., pp.205-242.

Brodmann, K. (1905) Beitrage zur histologischen Lokalisation der Grosshirnrinde. Dritte Mitteilung: Die Rindenfelder der niederen Affen. J. Psychol. Neurol. 4:177-226.

Bruce, C.J., Desimone, R., and Gross, C.G. (1981) Visual properties of neurones in a polysensory area in the superior temporal sulcus of the macaque. J. Neurophysiol. 46:369-384.

Burton, H., and Jones, E.G. (1976) The posterior thalamic region and its cortical projection in New World and Old World monkeys. J. Comp. Neurol. 168:249-302.

Burton, H., and Robinson, C.J. (1981) Organization of the SII parietal cortex: multiple somatic sensory representations within and near the second somatic sensory area of cynomologous monkeys. In: C.N. Woolsey (ed.) Cortical Sensory Organization, Volume 1, Multiple Somatic Areas. Humana Press, Clifton, N.J., pp.67-119.

Chavis, D.A., and Pandya, D.N. (1976) Further observations on corticofrontal connections in the rhesus monkey. Brain Res. 117:369-386.

Constanzo, R.M., and Gardner, E.P. (1980) A quantitative analysis of responses of direction-sensitive neurons in somatosensory cortex of awake monkeys. J. Neurophysiol. 43:1319-1341.

Duffy, F.H., and Burchfield, J.L. (1971) Somatosensory system: Organizational hierarchy from single units in monkey area 5. Science 172:273-275.

Ettlinger, G., and Garcha, H.S. (1980) Cross-modal recognition by the monkey: The effects of cortical removals. Neuropsychologia 18:685-692.

Fleming, J.F.R. and Crosby, E.A. (1955) The parietal lobe as an additional motor area. The motor effects of electrical stimulation and ablation of cortical area 5 and 7 in monkeys. J. Comp. Neurol. 10:485-517.

Friedman, D.P. (1978) Body somatotopy in the second somatic sensory cortex of the monkey. Soc. Neurosci. Abstr. 4:551.

Friedman, D.P. (1981) Body topography in the second somatic sensory area: monkey SII somatotopy. In: C.N. Woolsey (ed.) Cortical Sensory Organization, Volume 1, Multiple Somatic Areas. Humana Press, Clifton, N.J., pp.121-165.

Friedman, D.P. (1983) Laminar patterns of termination of cortico-cortical afferents in the somatosensory system. Brain Res. 273:147-151.

Friedman, D.P., Jones, E.G., and Burton, H. (1980) Representation pattern in the second somatic sensory area of the monkey cerebral cortex. J. Comp. Neurol. 192:21-41.

Friedman, D.P., Murray, E.A., and Mishkin, M. (1982) Cortico-limbic pathway for touch: Connections via somatosensory cortical fields in the lateral sulcus of the monkey. Soc. Neurosci. Abstr. 8:38.

Friedman, D.P., Murray, E.A., O'Neill, J.B., and Mishkin, M. (1986) Cortical connections of the somatosensory fields of the lateral sulcus of macaques: Evidence for a corticolimbic pathway for touch. J. Comp. Neurol. 252:323-347.

Goldberg, M.E., and Robinson, D.L. (1977) Visual responses of neurones in monkey inferior parietal lobule: The physiologic substrate of attention and neglect. Neurology 27:350.

Gross, C.G., Bruce, C.J., Desimone, R., Fleming, J., and Gatass, R. (1981) Cortical visual areas of the temporal lobe: Three areas in the macaque. In: C.N. Woolsey (ed.) Cortical Sensory Organization, Volume 2, Multiple Visual Areas. Humana Press, Clifton, N.J., pp.187-216.

Hartje, W., and Ettlinger, G. (1973) Reaching in light and dark after unilateral posterior parietal ablations in the monkey. Cortex 9:346-354.

Hyvarinen, J. (1981) Regional distribution of functions in parietal association area 7 of the monkey. Brain Res. 206:287-303.

Hyvarinen, J. (1982) The Parietal Cortex of Monkey and Man, Volume 8, Studies of Brain Function. Springer Verlag, New York Inc.

Hyvarinen, J., and Poranen, A. (1974) Function of the parietal associative area 7 as revealed from cellular discharges in alert monkeys. Brain, 97:673-692.

Hyvarinen, J., and Poranen, A. (1978a) Movement-sensitive and direction and orientation-selective cutaneous receptive fields in the hand area of the post-central gyrus in monkeys. J. Physiol. 283:523-537.

Hyvarinen, J., and Poranen, A. (1978b) Receptive field integration and submodality convergence in the hand area of the post-central gyrus of the alert monkey. J. Physiol. 283:539-556.

Hyvarinen, J., Poranen, A., Jokinen, Y., Naatanen, R., and Linnankoski, I. (1975) Observations on unit activity in the primary somesthetic cortex of behaving monkeys. In H.H. Kornhuber (ed.) The Somatosensory System. Georg Thieme Publishers, Stuttgart, pp.241-249.

Iwamura, Y., and Tanaka, M. (1978a) Postcentral neurons in hand region of area 2: Their possible role in the form discrimination of tactile objects. Brain Res. 150:662-666.

Iwamura, Y., and Tanaka, M. (1978b) Functional organization of receptive fields in the cat somatosensory cortex. I: Integration within the coronal region. Brain Res. 151:49-60.

Iwamura, Y., and Tanaka, M. (1978c) Functional organization of receptive fields in the cat somatosensory cortex. II: Second representation of the forepaw in the ansate region. Brain Res. 151:61-72.

Iwamura, Y., Tanaka, M., and Hikosaka, O. (1981) Cortical neuronal mechanisms of tactile perception studied in the conscious monkey. In: M. Sato and R. Norgren (eds) Brain Mechanisms of Sensation. Wiley, New York, pp.61-70.

Iwamura, Y., Tanaka, M., and Sakamoto, M. (1982) Comparison of finger representation pattern between area 3 and 1 of monkey somatosensory cortex (SI). Neurosci. Lett. Suppl. 9:112.

Iwamura, Y., Tanaka, M., Sakamoto, M. and Hikosaka, O. (1985a) Diversity in receptive field properties of vertical neuronal arrays in the crown of the postcentral gyrus of the conscious monkey. Exp. Brain Res. 58:400-411.

Iwamura, Y., Tanaka, M., Sakamoto, M., and Hikosaka, O. (1985b) Vertical neuronal arrays in the postcentral gyrus signalling active touch: A receptive field study in the conscious monkey. Exp. Brain Res. 58:412-420.

Jacobsen, S., and Trojanowski, J.Q. (1977) Prefrontal granular cortex of the rhesus monkey. I. Intrahemispheric cortical afferents. Brain Res. 132:209-233.

Jones, E.G. (1983) Lack of collateral thalamocortical projections to fields of the first somatic sensory cortex in monkeys. Exp. Brain Res. 52:375-384.

Jones, E.G., and Burton, H. (1976) Areal differences in the laminar distribution of thalamic afferents in cortical fields of the insular, parietal and temporal regions of primates. J. Comp. Neurol. 168:197-248.

Jones, E.G., Coulter, J.D., and Hendry, S.H.C. (1978) Intracortical connectivity of architectonic fields in the somatic sensory, motor, and parietal cortex of monkeys. J. Comp. Neurol. 181:291-348.

Jones, E.G., and Friedman, D.P. (1982) Projection pattern of functional components of thalamic ventrobasal complex on monkey somatosensory cortex. J. Neurophysiol. 48:521-544.

Jones, E.G., and Powell, T.P.S. (1969) Connexions of the somatic sensory cortex in the rhesus monkey. I. Ipsilateral cortical connexions. Brain 92:477-502.

Jones, E.G., and Powell, T.P.S. (1970a) An anatomical study of converging sensory pathways within the cerebral cortex of the monkey. Brain 93:793-820.

Jones, E.G., and Powell, T.P.S. (1970b) Connexions of the somatic sensory cortex of the rhesus monkey. III. Thalamic connexions. Brain 93:37-56.

Juliano, S.L., Hand, P.J., and Whitsel, B.L. (1983) Patterns of metabolic activity in cytoarchitectural area SII and surrounding cortical fields of the monkey. J. Neurophysiol. 50:961-980.

Kaas, J.H., Nelson, R.J., Sur, M., Lin C-S, Merzenich, M.M. (1979) Multiple representations of the body within the primary somatosensory cortex of primates. Science 204:521-532.

Kaas, J.H., Sur, M., Nelson, R.J., and Merzenich, M.M. (1981) The postcentral somatosensory cortex: multiple representations of the body in primates. In: C.N. Woolsey (ed.) Cortical Sensory Organization, Volume 1, Multiple Somatic Areas. Humana Press, Clifton, N.J., pp.29-45.

Latto, R. (1978) The effects of bilateral frontal eye-field, posterior parietal or superior collicular lesions on visual search in the rhesus monkey. Brain Res. 146:35-50.

Leinonen, L. (1980) Functional properties of neurones in the posterior parietal of area 7 in the awake monkey. Acta. Physiol. Scand. 108:301-308.

Leinonen, L. (1981) Functions of posterior parietal-temporoparietal cortex in the monkey. Academic dissertation, Helsinki.

Leinonen, L. (1984) Integration of somatosensory events in the posterior parietal cortex of the monkey. In: C. von Euler (ed.) Somatosensory mechanisms. MacMillan Press, London, pp.113-124.

Leinonen, L., Hyvarinen, J., Nyman, G. and Linnankoski, I. (1979) Functional properties of neurons in lateral part of associative area 7 in awake monkey. Exp. Brain Res. 34:299-320.

Leinonen, L., and Nyman, G. (1979) Functional properties of cells in anterolateral part of area 7 associative face area of awake monkeys. Exp. Brain Res. 34:321-333.

Leinonen, L., Hyvarinen, J., and Sovijarvi, A.R.A. (1980) Functional properties of neurones in the temporo-parietal association cortex of awake monkeys. Exp. Brain Res. 39:203-215.

Luh, K.E., Butter, C.M., and Buchtel, H.A. (1986) Impairment in orienting to visual stimuli in monkeys following unilateral lesions of the superior sulcal polysensory cortex.

Neuropsychologia 24:461-470.

Lynch, J.C., Mountcastle, V.B, Talbot, W.H., and Yin, T.C.T. (1977) Parietal lobe mechanisms for directed visual attention. J. Neurophysiol. 40:362-389.

Merzenich, M.M., Kaas, J.H., Sur, M., Lin C-S. (1978) Double representation of the body surface within cytoarchitectonic areas 3b and 1 in "SI" in the owl monkey (Aotus trivirgatus). J. Comp. Neurol. 181:41-74.

Merzenich, M.M., Sur, M., Nelson, R.J., and Kaas, J.H. (1981) Organization of the SI cortex: multiple cutaneous representations in areas 3b and 1 of the Owl monkey. In: C.N. Woolsey (ed.) Cortical Sensory Organization, Volume 1, Multiple Somatic Areas. Humana Press, Clifton, N.J., pp.47-65.

Mesulam, M.-M., Van Hoesen, G.W., Pandya, D.N., and Geshwind, N. (1977) Limbic and sensory connections of the inferior parietal lobule (area PG) in the rhesus monkey: A study with a new method for horseradish peroxidase histochemistry. Brain Res. 136:393-414.

Milner, A.D., Ockleford, E.M., and Dewar, W. (1977) Visuo-spatial performance following posterior parietal and lateral frontal lesions in stumptail macaques. Cortex 13:350-360.

Mishkin, M. (1966) Visual mechanisms beyond the striate cortex. In R. Russel (ed.) Frontiers of Physiological Psychology. Academic Press, New York, pp.93-119.

Mishkin, M. (1979) Analagous neural models for tactual and visual learning. Neuropsychologia 17:139-151.

Mountcastle, V.B., Lynch, J.C., Georgopoulos, A., Sakata, H., and Acuna, C. (1975) Posterior parietal association cortex of the monkey: Command functions for operations within extrapersonal space. J. Neurophysiol. 38:871-908.

Mountcastle, V.B., Talbot, W.H., Sakata, H., and Hyvarinen, J. (1969) Cortical neuronal mechanisms in flutter-vibration studied in nonanaesthetized monkeys. Neuronal periodicity and frequency discrimination. J. Neurophysiol. 32:452-484.

Mufson, E.J., Mesulam, M-M., and Pandya, D.N. (1981) Insular interconnections with the amygdala in the rhesus monkey. Neurosci. 6:1231-1248.

Murray, E.A., and Mishkin, M. (1984) Relative contributions of SII and area 5 to tactile discrimination in monkeys. Behav. Brain Res. 11:67-83.

Murray, E.A., Nakamura, R.K., and Mishkin, M. (1980) A possible cortical pathway for somatosensory processing in monkeys. Soc. Neurosci. Abstr. 6:654.

Pandya, D.N., and Kuypers, H.G.J.M. (1969) Cortico-cortical connections in the rhesus monkey. Brain Res. 13:13-36.

Pandya, D.N., and Seltzer, B. (1982) Association areas of the cerebral cortex. Trends Neurosci. 5:386-390.

Pandya, D.N., and Yeterian, E.H. (1985) Architecture and connections of cortical association areas. In: A.Peters and E.G. Jones (eds) Cerebral Cortex, Volume 4. Plenum Press, New York.

Paul, R.L., Merzenich, M., Goodman, H. (1975) Mechanoreceptor representation and topography of Brodmann's areas 3 and 1 of Macaca mulatta. In H.H. Kornhuber (ed.) The Somatosensory System. Georg Thieme Publishers, Stuttgart, pp.262-269.

Peele, T.L. (1944) Acute and chronic parietal lobe ablations in monkeys. J. Neurophysiol. 7:269-286.

Petrides, M., and Iverson, S.D. (1979) Restricted posterior parietal lesions in the rhesus monkey and performance on visuospatial tasks. Brain Res. 161:63-77.

Pohl, W. (1973) Dissociation of spatial discrimination deficits following frontal and parietal lesions in monkeys. J. Comp. Physiol. Psychol. 82:227-239.

Poranen, A., and Hyvarinen, J. (1982) Effects of attention on multiunit responses to vibration in the somatosensory regions of the monkey's brain. Electroencephalogr. Clin. Neurophysiol. 53:525-537.

Powell, T.P.S., and Mountcastle, V.B. (1959a) The cytoarchitecture of the postcentral gyrus of the monkey Macaca mulatta. Bull. Johns Hopkins Hosp. 105:108-131.

Powell, T.P.S., and Mountcastle, V.B. (1959b) Some aspects of the functional organization of the cortex of the postcentral gyrus of the monkey: a correlation of findings obtained in a single unit analysis with cytoarchitecture. Bull. Johns Hopkins Hosp. 105:133-162.

Randolph, M., and Semmes, J. (1974) Behavioural consequences of selective subtotal ablation in the postcentral gyrus of Macaca mulatta. Brain Res. 70:55-70.

Ratcliff, G., Ridley, R.M., and Ettlinger, G. (1977) Spatial disorientation in the monkey. Cortex 13:62-65.

Ridley, R.M., and Ettlinger, G. (1976) Impaired tactile learning and retention after removals of the second somatic sensory projection cortex (SII) in the monkey. Brain Res. 109:656-660.

Ridley, R.M., and Ettlinger, G. (1978) Further evidence of impaired tactile learning after removals of the second somatic sensory projection cortex (SII) in the monkey. Exp. Brain Res. 31:475-488.

Roberts, T.S., and Akert, K. (1963) Insular and opercular cortex and its thalamic projection in Macaca mulatta. Schweizer Arch. Neurol. Neurochirurg. Psychiatry 92:1-43.

Robinson, C.J., and Burton, H. (1980a) Organization of somatosensory receptive fields in cortical areas 7b, retroinsular, postauditory and granular insula of M. fascicularis. J. Comp. Neurol. 192:69-92.

Robinson, C.J., and Burton, H. (1980b) Somatic submodality distribution within the second somatosensory (SII), 7b, retroinsular, postauditory, and granular insular cortical areas of M. fascicularis. J. Comp. Neurol. 192:93-108.

Robinson, D.L., Goldberg, M.E., and Stanton, G.B. (1978) Parietal association cortex in the primate: sensory mechanisms and behavioural modulations. J. Neurophysiol. 41:910-932.

Sakata, H. (1975) Somatic sensory response of neurones in the parietal association area (area 5) of monkeys. In: H.H. Kornhuber (ed.) The Somatosensory System. Georg Thieme Publishers, Stuttgart, pp.250-261.

Sakata, H., and Iwamura, Y. (1978) Cortical processing of tactile information in the first somatosensory and parietal association areas in the monkey. In: G. Gordon (ed.) Active Touch. Pergamon Press, Oxford, pp.55-72.

Sakata, H., Shibutani, H., and Kawano, K. (1977) Spatial selectivity of 'visual' neurones in the posterior parietal association cortex of the monkey. Abstract for the 27th Int'l Congress of Physiol. Sci.

Sakata, H., Shibutani, H., and Kawano, K. (1978) Parietal neurones with dual sensitivity to real and induced movements of visual target. Neurosci. Lett. 9:165-169.

Sakata, H., Shibutani, H., and Kawano, K. (1980) Spatial proportions of visual fixation neurones in posterior parietal association cortex of the monkey. J. Neurophysiol. 43:1654-1672.

Sakata, H., Takaoka, Y., Kawarasaki, A., and Shibutani, H. (1973) Somatosensory properties of neurons in the superior parietal cortex (area 5) of the rhesus monkey. Brain Res. 64:85-102.

Schwarz, D.W.F., and Fredrickson, J.M. (1971) Tactile direction sensitivity of area 2 oral neurons in the rhesus monkey cortex. Brain Res. 27:397-401.

Seltzer, B., and Pandya, D.N. (1978) Afferent cortical connections and architectonics of the superior temporal sulcus and surrounding cortex in the rhesus monkey. Brain Res. 149:1-24.

Seltzer, B., and Pandya, D.N. (1984) Further observations on parieto-temporal connections in rhesus monkeys. Exp. Brain Res. 55:301-312.

Semmes, J., and Turner, B. (1977) Effects of cortical lesions on somatosensory tasks. J. Invest. Dermatol. 69:181-189.

Stein, J. (1976) The effect of cooling parietal lobe areas 5 and 7 upon voluntary movement in awake rhesus monkeys. J. Physiol. 258:62-63P.

Stein, J. (1978) The effect of parietal lobe cooling on manipulative behaviour in the conscious monkey. In: G. Gordon (ed.) Active Touch. Pergamon Press, Oxford, pp.79-90.

Sugishita, M., Ettlinger, G.,and Ridley, R.M. (1978) Disturbance of cage-finding in the monkey. Cortex 14:431-438.

Ungerleider, L.G., and Brody, B.A. (1977) Extrapersonal spatial orientation: The role of the posterior parietal, anterior frontal, and infero-temporal cortex. Exp. Neurol. 56:265-280.

Ungerleider, L.G., and Mishkin, M. (1982) Two cortical visual systems. In: D.J. Ingle, M.A. Goodale and R.J.W. Mansfield (eds) Analysis of Visual Behaviour. MIT Press, Cambridge, MA, pp.549-586.

Vogt, B.A., and Pandya, D.N. (1978) Cortico-cortical connections of somatic sensory cortex (areas 3, 1 and 2) in the rhesus monkey. J. Comp. Neurol. 177:179-192.

Vogt, C., and Vogt, O. (1919) Allgemeine Ergebnisse unserer Hirnforschung. J. Psychol. Neurol. 25:279-462.

Vogt, C., and Vogt, O. (1926) Die vergleichend-architektonische und die vergleichend-reiz-physiologische Felderung der Grosshirnrinde unter besonderer Berucksichtigung der menschlichen. Naturwissenschaften 14:1190-1194.

von Bonin, G., and Bailey, P. (1947) The Neocortex of Macaca mulatta. University of Illinois Press, Urbana.

Werner, G., and Whitsel, B.L. (1973) Functional organization of the somatosensory cortex. In: A. Iggo (ed.) Handbook of Sensory Physiology, Vol. II, Somatosensory System. Springer Verlag, New York, pp.621-700.

Whitsel, B.L., Petrucelli, L.M., and Werner, G. (1969) Symmetry and connectivity in the map of the body surface in somatosensory area II of primates. J. Neurophysiol. 32:170-183.

Whitsel, B.L., Roppolo, J.R., and Werner, G. (1972) Cortical information processing of stimulus motion on primate skin. J. Neurophysiol. 35:691-717.

Woolsey, C.N. (1958) Organization of somatic and motor areas of the cerebral cortex. In: H. Harlow and C.N. Woolsey (eds) Biological and Biochemical Bases of Behaviour. The University of Wisconsin Press, pp.63-81.

Yin, T.C.T., and Mountcastle, V.B. (1977) Visual input to the visuomotor mechanisms of the monkey's parietal lobe. Science 197: 1381-1383.

CHAPTER 4

Single unit processing of somatosensory information in macaque STS cortex: The role of 'expectation'.

4.1 Introduction

Recent evidence concerning the neural basis of tactual perception has led to the development of a neural model for sequential processing in which the primary somatosensory cortex (SI), secondary somatosensory cortex (SII), insular cortex and/or the parietal cortex are viewed as successive links in a neocortical-limbic pathway mediating tactile-affective associations (Mishkin, 1979). Absent from this tactile processing pathway is a region of temporal association cortex - the superior temporal sulcus (STS) - shown to be selective at the single-unit level for somesthetic stimuli (Bruce et al, 1981). The exact function of this area in tactile perception is unknown.

An accumulation of evidence supports the inclusion of SI, SII and insular cortex in the above scheme (reviewed in Chapter 3) and to some extent the posterior parietal cortex, although recent studies suggest that this area may be concerned more with multimodal spatial functions than unimodal tactual operations (Hyvarinen and Poranen, 1974; Leinonen et al, 1979; Lynch et al, 1977; Mountcastle et al, 1975). Evidence from single-unit studies for the inclusion of the STS in a tactual processing pathway is limited to a study of the polysensory STS in anaesthetized animals (Bruce et al, 1981). They observed that

somesthetic receptive fields were large, often including the whole body, and indicated that the cells were relatively unselective amongst tactile stimuli. But, there is compelling evidence that does suggest a role for the STS in tactual processing.

Mishkin (1979) has argued for a neural model of tactual perception analogous to that proposed for visual perception in which the striate, prestriate and inferior temporal areas are viewed as links to the limbic system mediating visual-affective associations. In the visual modality a central role has been postulated for the STS in the mediation of "higher perceptual functions" such as face and body movement perception and social communication. Evidence for such high-level analysis has come from single-unit recording studies (Perrett et al, 1982, 1984, 1985a,b), behavioural studies of the effects of STS ablation (see Chapter 6) and anatomical connectional studies (reviewed in Chapter 3). They imply that the STS could, through its projections to the limbic structures (Aggleton et al, 1980), function as a final link in visual processing.

The connectional studies also stress the intermodal convergence of sensory information witnessed at the single-unit level in the STS (Jones and Powell, 1970) which receives projections from the insular cortex (Friedman et al, 1986), the inferior temporal cortex (e.g. Jones and Powell, 1970; Jones and Burton, 1976; Seltzer and Pandya, 1978) and posterior parietal cortex (e.g. Jones and Powell, 1969, 1970; Aggleton et al, 1980). These studies highlight the capability of this area of association cortex in providing a route for integrated multimodal information to the limbic system.

From the comparable neural models for tactual and visual processing, Murray and Mishkin (1984) further proposed that the posterior insular cortex and the anterior inferior temporal cortex (TE) might be analogous final cortical links in the sensory-limbic pathways serving the tactual and visual modalities respectively. Although the STS is not part of Mishkin's pathways, it is in a position to serve as an additional higher order processing area passing on static or dynamic visual information received from areas TE, MT (V5), and MST (V6) (Zeki, personal communication) to the limbic system. In the same way, the STS is in a position to provide an equivalent link between the tactual and limbic systems, passing highly processed tactual information received from the insular cortex and possibly the posterior parietal cortex to the limbic structures.

The main impetus for an investigation into the somatosensory properties of single cells in the cortex of the STS (employing microelectrode recording technique in awake, behaving monkeys) was therefore to determine the contribution (if any) made by this region of association cortex to the neural organization underlying tactile processing. For each cell isolated a variety of different stimuli were used to get a comprehensive profile of cellular functions during natural behaviour. There would have been no point in looking at some preselected relationships between a behaviour and neuronal activity as the dimensions of touch important to these cells were relatively unknown. As Fetz (1981) pointed out, documenting the activity of cells in a given region in relation to one particular behavioural response ignores the potential involvement of these same cells in many other behavioural functions.

During the investigation it soon became apparent that STS neurones were dependent on the 'expectedness' of a stimulus such that neurones discharged or responded to somesthetic stimuli only when stimulation was 'unexpected' (Mistlin et al, 1986). A study was therefore made as to the relationship between the activity of the neurones and the predictability of the stimulus defined by either the tactual or visual modalities. Since this area of cortex is polymodal, a separate aspect of the study investigated the extent to which visual response selectivity was associated with the tactile responses found.

The results of this study provide evidence for the involvement of the STS in tactual processing through the sophisticated coding of a dimension previously unreported. The uniqueness of the concept of expectedness in this context is discussed, as is the information needed for such neural selectivity, and the possible function of discriminating expected and unexpected tactile stimulation. Such considerations (in conjunction with connectional data reviewed in Chapter 3) are used to speculate a position for the STS in a neural pathway for tactual perception.

4.2 General Methods

Single unit recording in conscious, behaving monkeys was performed using the standard techniques described in Chapter 2. The main body of this experimental work was investigated in one macaque monkey, Fiona (F), over a period of one and a half years, although

quantitatively similar results were obtained in a second monkey (P). As daily recording sessions, each lasting several hours, leads to the accumulation of a very large data base for each experimental animal, the use of more subjects (although preferable) was not considered essential. It is important to consider that such recording techniques require a large investment of time and wo/manpower and that the financial, but more importantly, the humane cost of experimental animals are limiting factors. Indeed, Lemon (1984) notes that one of the many advantages with the technique of chronic single unit recording in conscious animals is that it 'greatly reduces the number of experimental animals required to provide the answer to a scientific question'.

It is of interest to note that one reason the somatosensory properties of the cells in the STS were investigated in detail was because Fiona, a rhesus macaque, quickly accepted being handled. A great deal of time was spent with the animal when in her home cage, familiarizing her with and generally encouraging her to accept handling by the experimenter. That the monkey was not unduly disturbed by this handling is indicated by the fact that in response to it, the monkey often groomed the experimenter. Such passive acceptance, in this monkey, of handling by the experimenter made experimental testing for somatosensory properties of cells in a conscious monkey a far easier task than might otherwise have been expected.

4.2.1 Procedure for investigation of cell properties

Immediate access to all parts of the monkey's body surface, for investigation of the somatosensory properties of cells, was restricted due to the primate chair's construction. This arrangement did however divide the monkey's body into three working receptive field zones: The head; the upper torso - shoulders, chest, back, arms, hands; and the lower torso - hips, legs, feet, tail. The face, lower torso and hands were always accessible for somatosensory stimulation and the rest of the body could be made available by opening out the front section of the primate chair (Figure 2.1). For the majority of the somatosensory testing the monkey's vision was obscured by placing a large aperture shutter across the viewing portion of the chair. A number of objects (described separately) were used for tactile stimulation of the monkey's body surface, but most commonly, the experimenter's hands, acting as tactile probes, were used to rapidly assess the properties of the cell which could then be investigated in more detail.

4.2.2 Stimuli

(a) Tactile stimuli

A number of objects were selected as tactile stimuli which differed from one another in shape, size and texture; these included fur (coarse or fine), wood, metal bars, paper, cloth and parts of the monkey's primate chair. In addition to classification according to their physical properties, these stimuli were labelled as 'expected' or 'unexpected' tactile stimuli. Functional definitions of these terms are given below.

Unexpected stimuli: For a tactile stimulus to be unexpected it was required that no information about its presence, location or nature was immediately available prior to stimulation. With vision excluded (and any obvious auditory cues minimized) any object used passively to stimulate the monkey's body surface would then be unexpected by this definition. Tactile stimulation as a result of the monkey's own movements could also be unexpected. For example, when the monkey actively moved her legs in her immediate extrapersonal space and encountered an unfamiliar object or a familiar object in a novel location the resulting tactile stimulation would be unexpected.

Expected stimuli: For a tactile stimulus to be expected, specific information about the stimulus was required in order that the impending tactile collision and subsequent stimulation could be predicted. With vision excluded an expected stimulus could only be defined for active stimulation; i.e. only when the monkey actively encountered an object of which it had had extensive previous knowledge (e.g. of its location and its nature) would the tactile stimulation be expected. In this condition (i.e. vision excluded) passive tactile stimulation could not be expected as no information would be available to predict the tactile collision. However, by allowing the monkey to see the tactile stimulus, all the necessary information would be available by which the monkey could determine the spatial and temporal characteristics of the tactile collision and subsequent stimulation. Thus, passive (and active) touch 'in sight' would be expected.

During active touch, when the monkey's own movements resulted in

tactile stimulation, the monkey's tactile contact with parts of the primate chair was classified as expected; whereas contact with objects placed on the perch unbeknown to the monkey were unexpected.

(b) Visual stimuli

A large collection of inanimate 3-dimensional objects which varied along different visual dimensions such as size, shape, colour, surface pattern and texture were available as visual stimuli. In addition, animate stimuli comprised whole bodies or parts of the body (e.g. face, arm, leg) of both monkeys and humans.

4.2.3 Stimulus presentation and testing protocol

Tactile stimulation of the monkey was applied directly by the experimenter for a short time duration (up to 1s) primarily to investigate responses to stimulation onset, and a long duration (up to 5s) to look at responses to stimulation offset.

The majority of tactile testing was conducted with the monkey unable to see the source of the stimulation, a shutter-restricted view. The shutter was removed to allow the observing monkey to see the approaching stimulus. Visual stimuli were presented to the monkey from behind the shutter for duration of its opening (1s). These stimuli were presented against a uniform background approximately 0.3-1m from the monkey. Slides were back projected onto a white screen 1-3m from the monkey.

Visual stimuli were presented in a pseudorandom order with a variable interstimulus interval of 3-30s. The number of trials was dependent on the quality of the cell signal and the duration it was held; but where possible an average of 10 trials was collected for each test condition. Data analysis is described in Chapter 2.

A protocol of somatosensory testing was performed for each cell investigated which involved: (a) touching and removing touch from the body surface (skin and hairs); (b) applying deeper pressure changes to the skin (including stroking the body surface; and (c) moving the monkey's joints. For all cells equivalent somatosensory stimulation through the monkey's active movements was investigated. If a cell responded to any of these types of stimulation, a number of features were investigated:

(1) whether the cell responded to stimulation over the whole body surface or whether the receptive field of the cell was limited to a specific body part;

(2) whether the cell's response was restricted to stimulation by a particular type of stimulus (e.g. shape, size or texture of the stimuli);

(3) the time-course of the cell's response - its onset latency and the duration of the response (i.e. transient or sustained);

(4) whether the cell was selective for the onset or offset of tactile stimulation;

(5) whether the cell's response was excitatory or inhibitory relative to the cell's spontaneous activity when no tactile stimulus was applied;

(6) whether the cell's response habituated over time or with repeated

stimulation;

(7) whether a cell sensitive to somatosensory stimulation exhibited a visual response and if visual stimulation interacted with tactile stimulation; and finally

(8) whether a cell discriminated between 'unexpected' and 'expected' tactile stimulation.

(These features were incorporated into an information sheet [Appendix B] so that the data for every somatosensory cell on each track were readily available.)

The interaction between visual and tactile stimulation was investigated for cells using the procedure set out below. With a panel (5cm square) cut out of the front section of the primate chair (see Figure 2.1) through which the monkey could reach one arm, the monkey was encouraged to reach up for pieces of food (held in her view) and feed herself. Four conditions were then tested:

(1) passive (expected) touch, in sight - the monkey reached up towards a piece of food and with her arm stationary was touched by the experimenter;

(2) passive (unexpected) touch, out of sight - with vision excluded (by a blank piece of card, 15cm square, placed in front of the monkey's face) the monkey's arm was again touched by the experimenter;

(3) active (expected) touch, in sight - the monkey reached towards a piece of food and en route made a tactile encounter with the experimenter's hand;

(4) active (unexpected) touch, out of sight - with vision excluded (as in (2)), while reaching up the monkey again encountered the experimenter's hand.

A purely visual protocol of testing for each somatosensory cell was also employed, which involved: (a) presenting a number of objects statically to the monkey; and (b) presenting a variety of movements (of objects) to the monkey (e.g. translate up/down, left/right and towards/away from the monkey).

So, if in addition to a somatosensory response a visual response was observed, the following features were investigated (also Appendix B):
(1) whether the cell was selective for static or dynamic information;
(2) whether the cell's response was excitatory or inhibitory (relative to the cell's spontaneous activity when no visual stimulus was present);
(3) whether the cell was form selective; and lastly
(4) if the cell was motion sensitive, whether it showed directional selectivity.

If a cell's signal to noise ratio exceeded 2:1 on presentation of any tactile or visual stimulus, that cell was classified accordingly, i.e. tactile and/or visual. Further selectivity of the cell was confirmed as a consistently increased or decreased firing rate (compared to the cell's spontaneous level of activity) to a particular type or set of stimuli.

4.3 Results

In this study, 135 microelectrode penetrations were directed to

traverse the anterior upper bank of the superior temporal sulcus (STS) in the temporal lobe; 1553 cells in total were isolated and studied. Of 1087 cells tested for sensitivity to somaesthetic stimulation, 197 cells (18.1%) with somatosensory properties were found. It is this population of cells that will be described.

4.3.1 Histology

The majority of neurones observed with somatosensory properties (and associated visual properties) were located in the anterior, upper bank of the STS cortex (Figure 4.1). They were found in areas corresponding to the regions TPO and PGa defined by Seltzer and Pandya (1978, 1984); an area equivalent to that described as STP by Bruce et al (1981).

Recordings were made between 2.5 and 11.5mm anterior of the inter-aural plane. The somatosensory neurones were very highly concentrated between 7 and 9mm in the upper bank only of the STS, and were virtually distinct from the more medial face-sensitive cells recorded and reported in Chapter 7.

4.3.2 Classification of neurones

Three types of somatosensory response were identified and classified independently as tactile, joint and vibration neurones (see Table 1). (Note that the convergent neurones were taken into account when

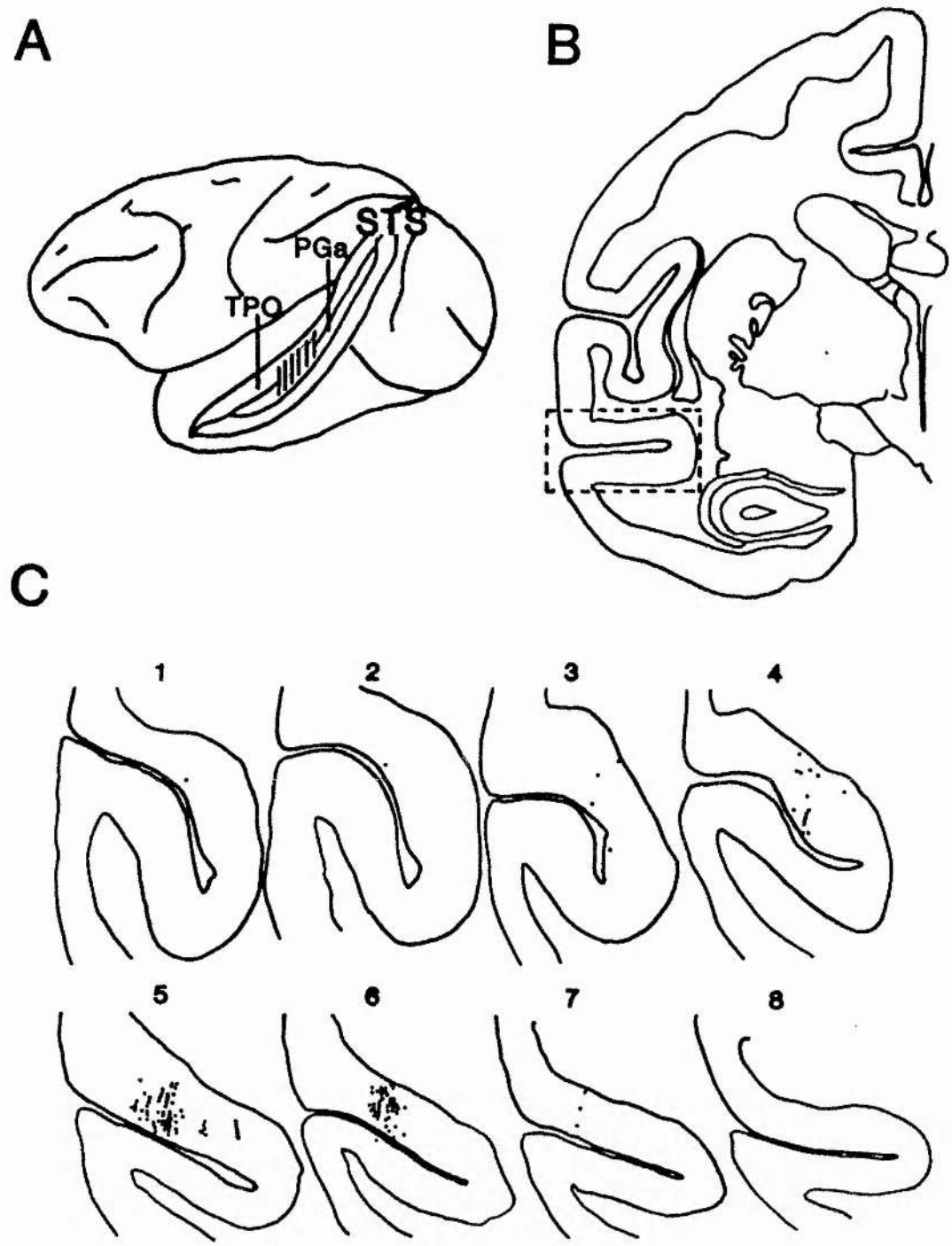


Figure 4.1 Histological reconstruction of the recording area. A, schematic drawing of a saggital view of a rhesus macaque brain showing the extent (cross-hatching) of the recording area along the upper bank of the superior temporal sulcus (STS) opened out to reveal the regions TPO and PGa (defined by Seltzer and Pandya, 1978, 1980). B, a coronal section of the monkey's right hemisphere indicates that area shown in the enlarged sections in C. C, the location of neurones with somatosensory responses are shown by filled circles on the sections 1-8 taken at 2.5-11mm anterior to the interaural plane in approx. 1mm steps.

Table 1 Classification of somatosensory neurone types recorded in the superior temporal sulcus

Description of neurone type	Number of cells	% of (1)
(1) Somatosensory neurones	197	
I Tactile neurones	188*	95.4
a. Neurones responding to cutaneous stimuli alone	160	81.2
II Joint neurones	29*	4.1
a. Neurones responding to joint movement alone	7	3.5
III Vibration neurones	13*	0.5
a. Neurones responding to vibration alone	1	0.5
IV Convergent neurones	29	14.7
a. Neurones responding to cutaneous stimuli and joint movement	17	8.6
b. Neurones responding to cutaneous stimuli and vibration	7	3.5
c. Neurones responding to joint movement and vibration	1	0.5
d. Neurones responding to cutaneous stimuli, joint movement and vibration	4	2.0

collating the total number of tactile, joint and vibration neurones.) The majority of cells observed (188/197, 95.4%) fell into the category of tactile neurones. Of these cells (I in Table 1) the greatest proportion of neurones (160/197, 81.2%) were those responsive only to cutaneous stimulation, not joint movement or vibration. This population of cells included those which responded to the onset (touch) or offset (detouch) of tactile stimulation in their receptive field (140/188); those which responded only to a movement of the stimulus along the skin , i.e. stroking (9/188); and those that could not be driven by light cutaneous stimuli, but did respond to the palpation (or gentle squeezing) of deeper tissues e.g. muscles, ligaments or tendons (11/188). Note, the cells responding to movement along the skin did not differentiate between different shapes of the moving stimuli. Indeed, none of the somatosensory cells observed in this study were noted to differentiate between simple stimulus parameters such as the shape, size or texture of the tactile stimulus.

An example of a cell (F012) that responded to being touched by a variety of different textured objects is shown in Figure 4.2. This cell responds significantly ($p<0.01$ Newman-Keuls each comparison) to either a wood, fur or metal tactile stimulus. No significant difference between these stimuli was evident. (The dimension of the stimulus that is important to these neurones is presented in 4.3.5.)

Twenty-nine cells were activated by passive movements of the monkey's joints with a proportion of these cells (7/29, 24.1%) responding only to joint movement and not to cutaneous stimulation or vibration. Similarly, 13 cells were responsive to the vibration of the monkey's

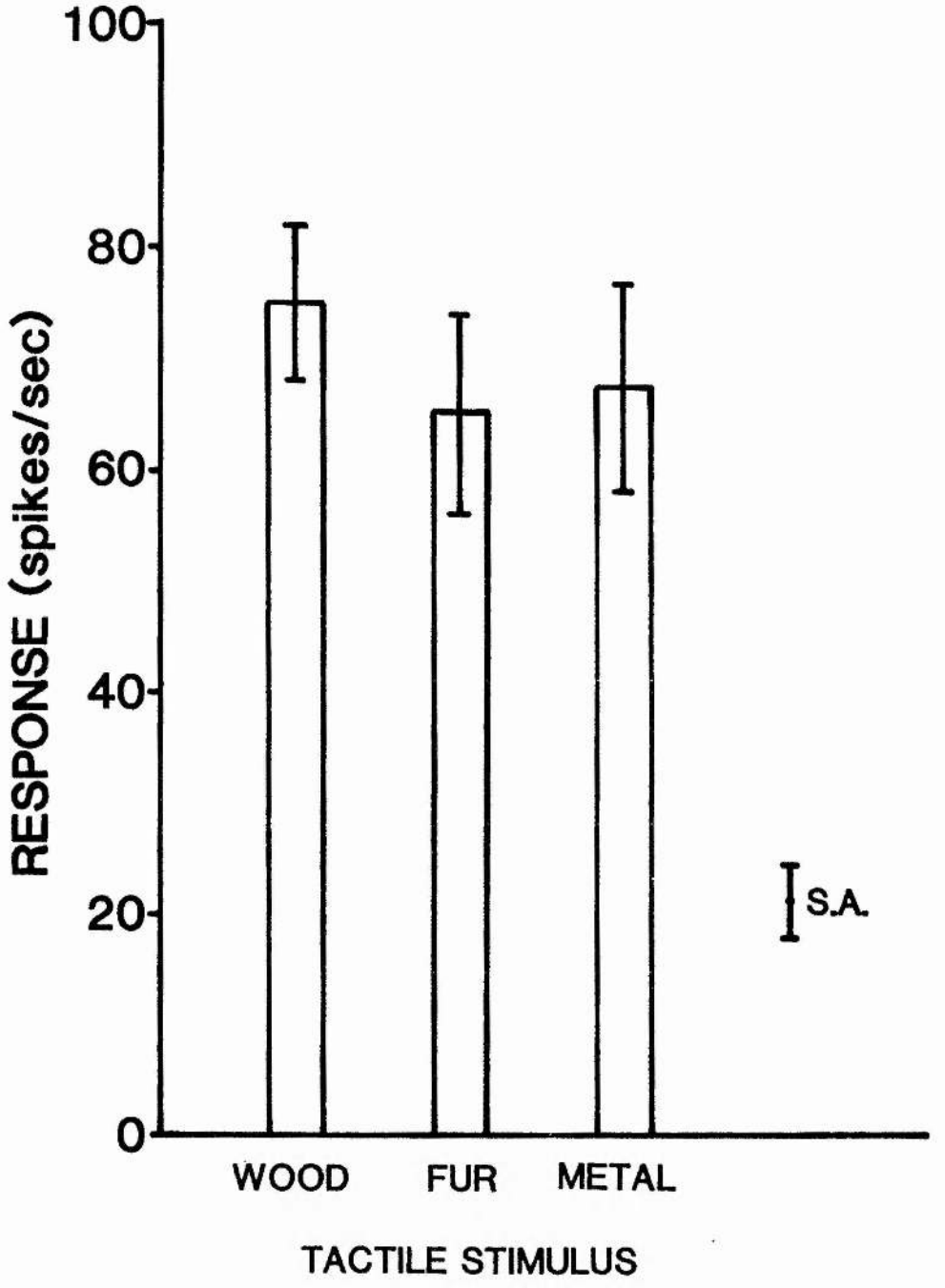


Figure 4.2 Response of one cell, F012, to tactile stimulation irrespective of the physical nature of the stimulus. The cell responds to touch with materials as diverse as wood, fur and metal. S.A., spontaneous activity. (Number of trials per condition (N)=6,5,6,6, overall effect of conditions $F=10.6$, $df=3,19$, $P<0.01$.)

immediate environment, with one cell responding to vibration but not cutaneous stimulation or joint movement. Convergent neurones comprised those cells with sensitivity to more than one submodality (see Table 1). The majority of these neurones (17/29, 58.6%) responded to cutaneous stimulation and joint movement, while seven neurones responded to cutaneous stimulation and vibration, one neurone to joint movement and vibration and four neurones to all three submodalities. It is possible that these figures are not precisely representative of the proportions of cells with such properties as for a few cells it was difficult to identify whether the cell was sensitive, for example, to joint movement or deep cutaneous stimulation, or vibration or light cutaneous stimulation. However, for most cells this discrimination was possible and the existence of cells sensitive to vibration but not light cutaneous stimulation or sensitive to joint movement but not deep cutaneous stimulation confirmed these cells' independent properties.

4.3.3 Temporal characteristics

Each tactile cell responded to stimulation with an ON response, an OFF response, or a combined ON-OFF response, which could be excitatory, inhibitory or both. The terms were defined as follows:

1) ON response; the onset of tactile stimulation (touch) produced a change in the cell's discharge rate

2) OFF response; the offset of tactile stimulation (detouch) produced a change in the cell's discharge rate, and

3) ON-OFF response; both the onset and offset of tactile stimulation

(touch/detouch) produced a change in the cell's discharge rate.

These responses were defined as excitatory or inhibitory if the firing rate of the cell was increased above or decreased below its spontaneous activity, respectively. Schematic representations of the possible combinations of responses are illustrated in Figure 4.3 which in conjunction with Table 2 gives an exhaustive break down of the cell responses observed. (Data for the tactile cells only are depicted here.)

Considering ON, OFF and ON-OFF responses, three-quarters of the tactile cells (148/188, 78.7%) were observed to have an excitatory response to touch and 18 cells (9.6%) an inhibitory response to touch. Similarly, 36 cells (19.1%) were observed to have an excitatory response to detouch and 5 cells (2.7%) an inhibitory response to detouch. For both touch- and detouch-sensitive cells the proportion of cells with an inhibitory response to tactile stimulation was small. This may be explained in part by the fact that spontaneous activity for the somatosensory neurones was low, (mean spontaneous activity +/-1S.D.=11.8+/-8.8 spikes/second, n40); so, as a consequence of this, an inhibition or decrease in the firing rate was difficult to discern. It is possible, therefore, that some inhibitory responses when present went undetected. For further data treatment, response categories 1)a and 3)c, and 2)a and 3)d (from Table 2) are grouped together (Figure 4.3). (If the inhibitory response was overlooked then a combined ON-OFF response such as 3)c or 3)d might have been classified as a pure ON or OFF response according to its excitatory characteristic.)

Table 2 Response characteristics of the tactile neurones observed in the superior temporal sulcus

Description of neuronal responses	Number of cells	% of (I)
I Tactile neurones	188	
1) ON response	147	78.2
a. Excitatory	139	73.9
b. Inhibitory	8	4.3
2) OFF response	22	11.7
a. Excitatory	22	11.7
b. Inhibitory	0	0.0
3) ON-OFF response	19	10.1
a. ON, OFF excitatory	5	2.7
b. ON, OFF inhibitory	1	0.5
c. ON excitatory, OFF inhibitory	4	2.1
d. ON inhibitory, OFF excitatory	9	4.8

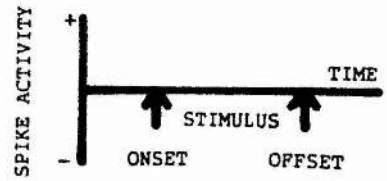
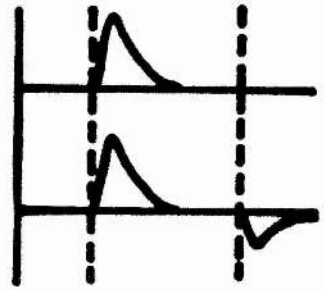
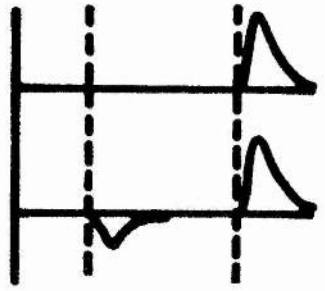
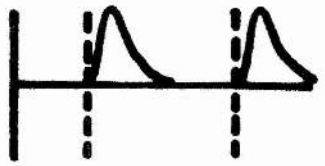
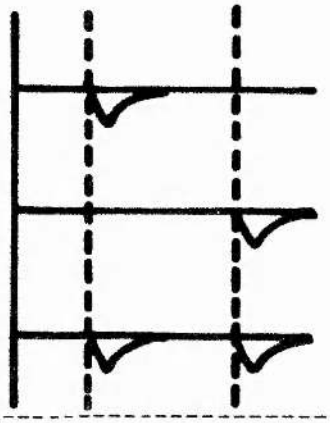
Response category	Response characteristic	Schematic representation of cell responses	Number of cells
			
1) a.	T+		139
3) c.	T+ DT-		4
2) a.	DT+		22
3) d.	T- DT+		9
3) a.	T+ DT+		5
1) b.	T-		8
2) b.	DT-		0
3) b.	T- DT-		1

Figure 4.3 Schematic representation of the possible combinations of temporal characteristics defining the types of somatosensory response found in the STS. The response category corresponds to Table 2. (T, touch; DT, detouch; +, excitatory; -, inhibitory.)

In Figure 4.3 the schematic representations of the cell responses have been shown to be transient. This was true for the majority of cells (177/188, 94.1%) but eleven neurones exhibited a relatively sustained response lasting 1-5 seconds. Examples of the time course of two cells' transient, excitatory responses sensitive (A) to touch (F034) and (B) to detouch (F094) are illustrated as post-stimulus time histograms in Figure 4.4. The onset latency of the response in (A) for passive expected touch was 46 ms and 64 ms for active unexpected touch. In (B) the onset latency for passive unexpected detouch was 16 ms. (The cells' onset latency was calculated as the value at which the response exceeded the cells' spontaneous activity +/-1.96S.D.) The onset of tactile stimulation was at 0ms with the offset variable between 100 ms and 500ms.

Figure 4.4 (A-B) demonstrates only the time-course of these cells' responses, it does not indicate whether these cells were only responsive to the onset (A) or offset (B) of tactile stimulation. Figure 4.4 (C-D) illustrates the form of response the cells in (A) and (B) exhibited. The cell (F056A) depicted in (C) gave a significantly greater response ($p<0.01$) to touch, compared with detouch. The reverse was true for the cell (F056B) in (D) where a significantly greater response ($p<0.01$) was observed for detouch. The response to neither detouch in (C) nor touch in (D) was significantly greater than the cells' spontaneous activity. The close relationship of the neural responses to the onset or offset of tactile stimulation strongly suggests that the cellular discharges were related to the tactile stimulus itself rather than an emotional response triggered by the stimuli, or a motor response. Of all the somatosensory neurones (197

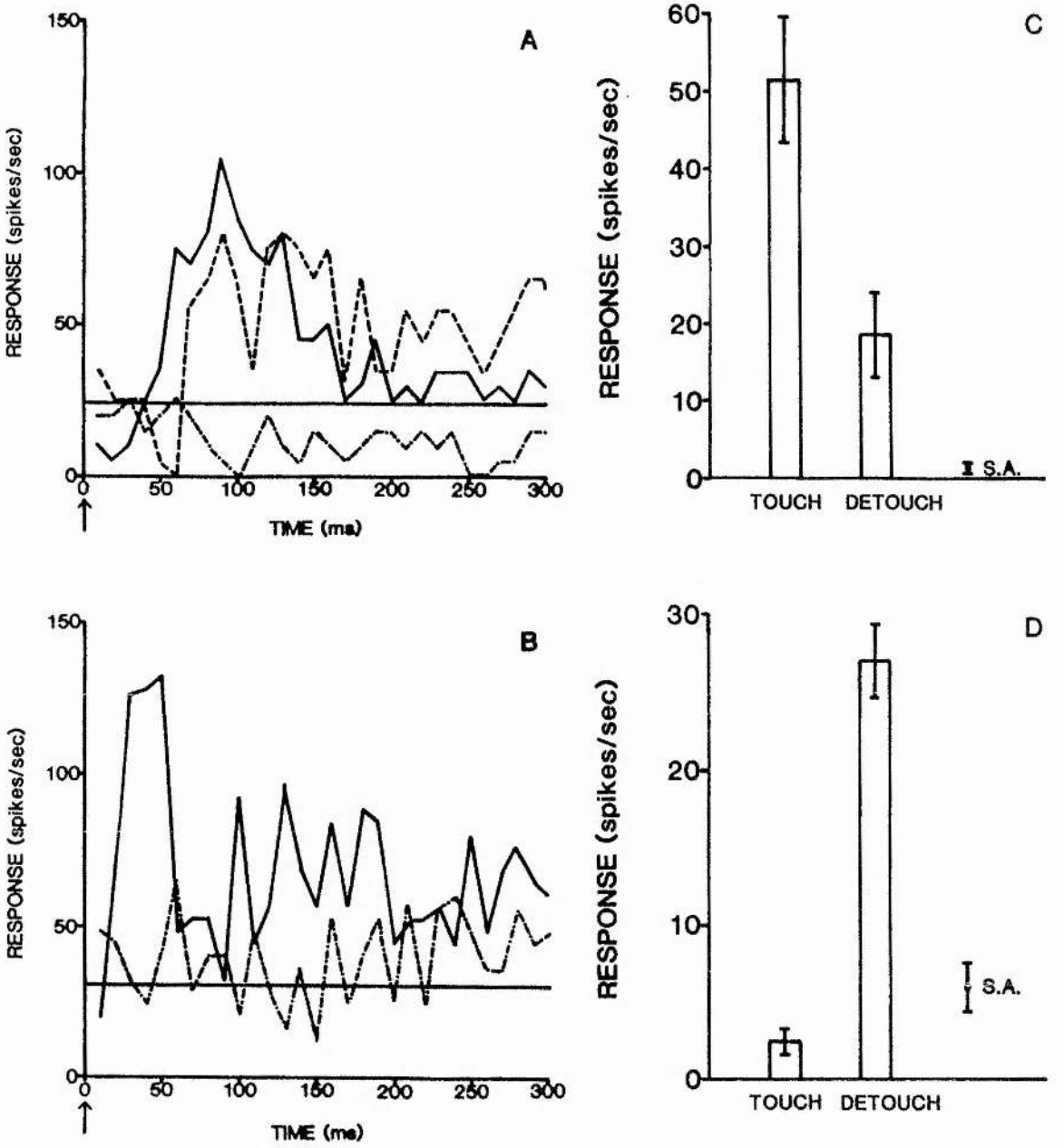


Figure 4.4 Response selectivity and time-course of cells sensitive to either the onset (touch) or offset (detouch) of tactile stimulation. Left: The post-stimulus time histograms indicate the response latencies for (A) cell F034, sensitive to unexpected touch (N=5, F=16.1, df=8,32, P<0.01); and (B) cell F094, sensitive to unexpected detouch (N=5, F=12.9, df=4,16, P<0.01). The arrows indicate the onset of tactile stimulation; solid line, passive unexpected tactile stimulation; dashed line, active unexpected stimulation; chaindotted line, active expected stimulation; solid horizontal line, the spontaneous activity level of the cell (+/-1.96 S.D.). Right: The histograms (C) and (D) represent the form of response exhibited by the cells in (A) and (B) respectively; where (C) cell F056A responds to touch but not detouch (N=10, F=21.2, df=2,18, P<0.01), and (D) cell F056B responds to detouch but not touch (N=10, F=50.5, df=2,18, P<0.01). S.A., spontaneous activity.

cells) only nine (4.6%) were noted to discharge to the monkey's active motor movements. For eight of these cells this response was in addition to a tactile response observed when the monkey's limbs were stationary.

For the majority of cells (184/197, 93.4%) responsiveness to somatosensory stimulation was a stable and repeatable finding often throughout testing periods lasting one or two hours. With repeated stimulation of a part of the monkey's body surface (a maximum of 20-50 trials) responses showed some variation in magnitude but were nearly always present and substantial. Only 13 cells showed a tendency for responsiveness to decline to the level of the cells' spontaneous activity. Habituation of the response in these cells occurred most frequently in 2-10 trials.

4.3.4 Receptive field

The somatosensory cells in all three classes - tactile, joint and vibration - had large receptive fields. Virtually the whole body surface constituted the receptive field for tactile and vibration sensitive cells and joint sensitive cells were responsive to the movement of any joint. The receptive fields of 18 tactile cells were extensively examined and this revealed one area of the body surface that was occasionally excluded from the receptive field. Considering the body surface as broadly divided into three zones - the face and the upper and lower torsos (see 4.2.1) - the receptive field of two-thirds of these cells (12/18, 66.7%) included both the upper and

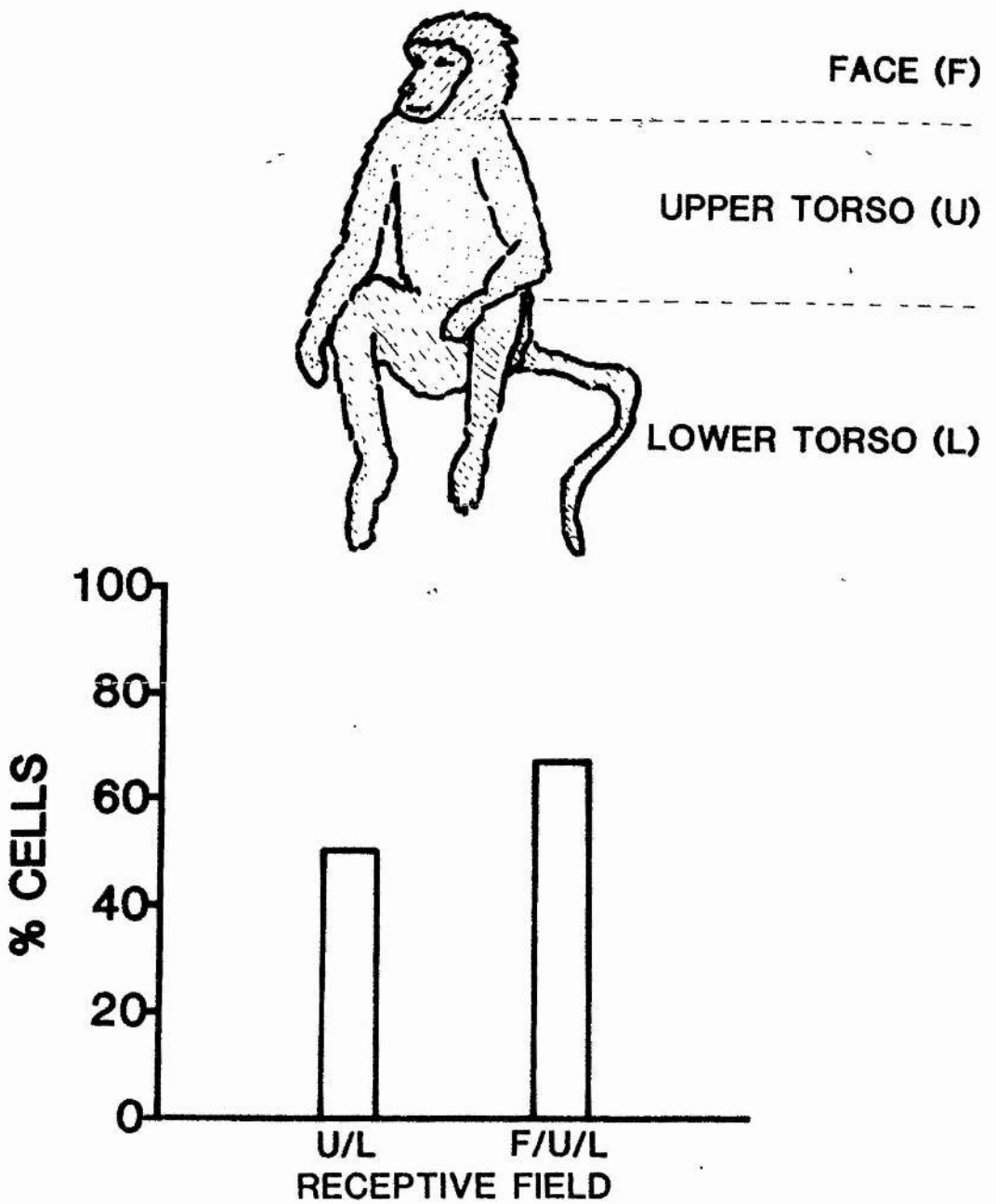


Figure 4.5 Frequency of STS neurones responsive to somatosensory stimulation with receptive fields including the whole (F/U/L) or part (U/L) of the body surface.

lower torso of the monkey's body; however, the receptive field of half of the cells (9/18, 50%) did not include the face (illustrated in Figure 4.5). These proportions of cells differed significantly ($p<0.05$, two way chi-square test of association, 1 degree of freedom (df), observed $x = 6.5143$). Three neurones possessed a receptive field limited to the chest and underarm surface.

4.3.5 Sensitivity to the expected/unexpected dimension of touch

(a) Touch out of sight

With vision excluded, 107 cells (of 111 tested, 96.4%) responded to unexpected tactile stimuli. Of 85 cells tested with both unexpected and expected stimuli, a greater response to unexpected tactile stimuli was observed for 84 cells (98.8%) where the response to expected tactile stimuli was significantly reduced or within the cells' spontaneous activity. Those cells that did not exhibit this sensitivity (5 cells) gave an equivalent response to both expected and unexpected tactile stimuli. No cells were observed with a reverse selectivity, i.e. no cells responded to expected stimuli more than unexpected stimuli. Figure 4.6 illustrates the selectivity of two cells (A, touch-sensitive cell; B, detouch-sensitive cell) for an unexpected tactile stimulus. Figure 4.6A demonstrates clearly that whether tactile stimulation was passive or active, it is the expected/unexpected dimension of touch that is important to the cell (F026). A significantly larger response was observed to both passive and active unexpected touch ($p<0.01$ each comparison) compared with

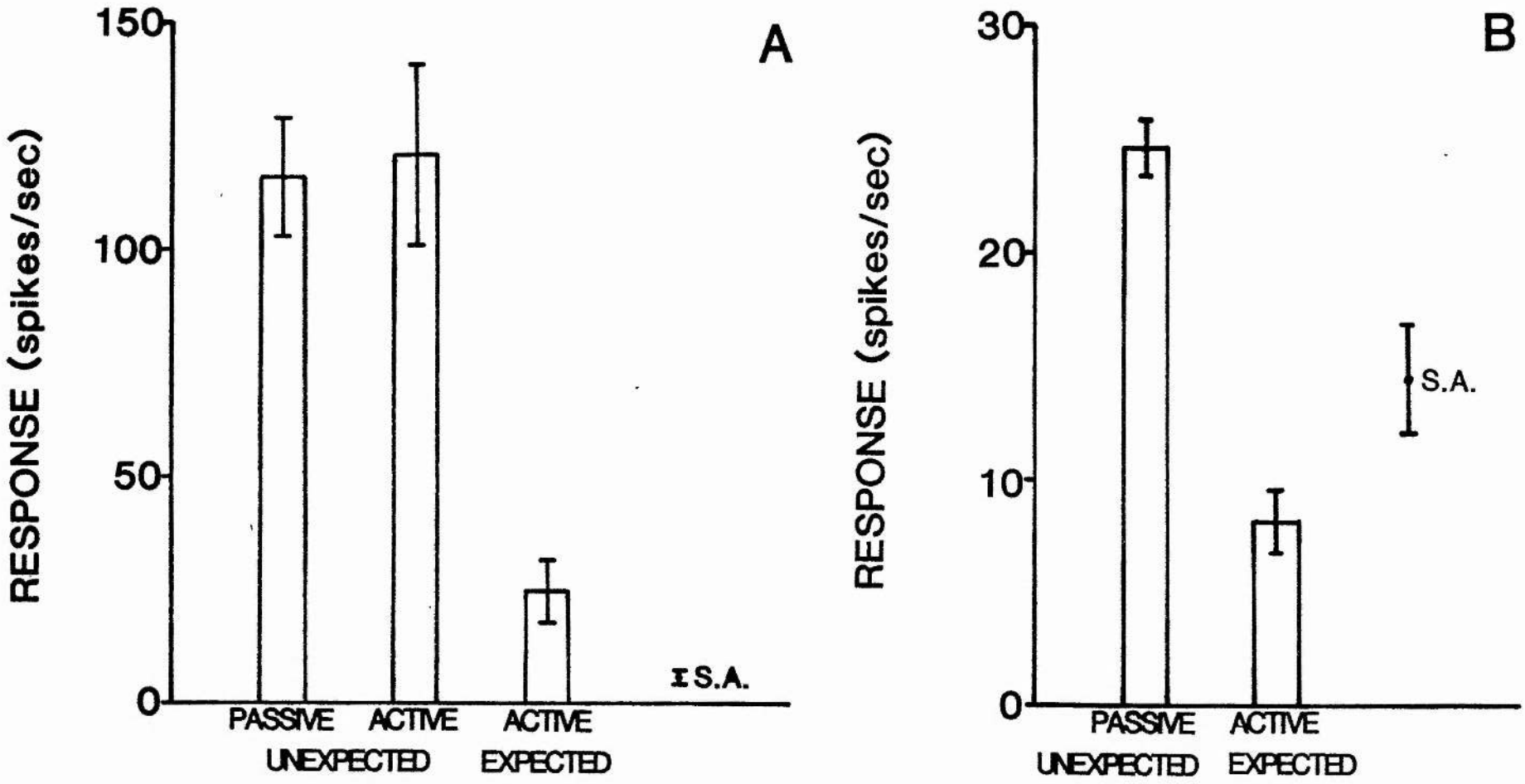


Figure 4.6 Differential responses of two cells to the unexpected dimension of tactile stimulation independent of the active or passive nature of the stimulation. A, touch-sensitive cell, F026 (N=5,5,6,8, F=32.6, df=3,20, P<0.01); B, detouch-sensitive cell, F106 (N=10, F=19.9, df=2,18, P<0.01). S.A., spontaneous activity.

active expected touch and the cell's spontaneous activity. No significant difference between passive and active unexpected touch, or expected touch and the cell's spontaneous activity was found.

The same form of response is indicated in Figure 4.6B for the detouch-sensitive cell F106, where a significantly larger response ($p<0.01$ each comparison) was observed for passive unexpected detouch. For this cell, active expected detouch also produced a small but significant effect on response ($p<0.05$) attributable to the depression of firing rate below spontaneous activity. Active unexpected detouch as a stimulus category cannot exist, as active removal of a part of the monkey's body surface from an object is under the monkey's motor control and therefore, intuitively, could never be unexpected.

A comparable discrimination between unexpected and expected stimuli was observed for a somatosensory cell (F066) sensitive to vibration. (The cell's response was not significantly affected by unexpected touch or joint movement.) Figure 4.7 shows that unexpected vibration of, for this cell, the monkey's foot perch elicited a significantly larger response ($p<0.01$ each comparison) than expected vibration of the same stimulus caused by the monkey's own movements, or the cell's spontaneous activity ($p<0.01$). Expected vibration did not affect the cell's response.

(b) Touch in sight

The somatosensory responses observed to tactile stimulation out of sight were compared with responses to the same stimulation in sight of the monkey, for 32 cells. Of these neurones, 23 (71.9%) were

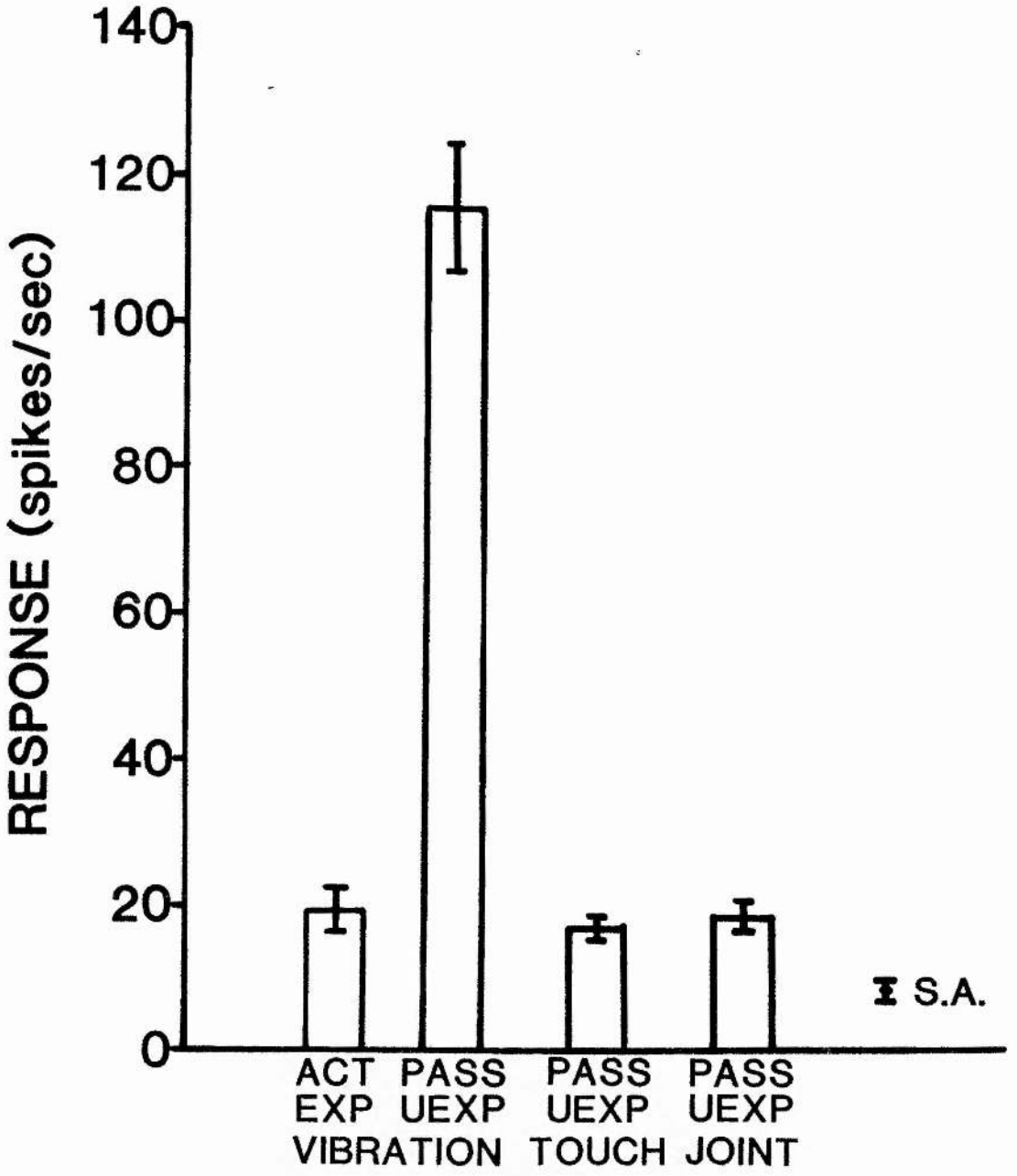


Figure 4.7 Response to unexpected tactile stimulation for one cell, F066, sensitive to vibration, rather than touch or joint movement. The active (ACT) or passive (PASS) nature of the stimulation is unimportant relative to the expected/unexpected (EXP/UEXP) dimension of stimulation. S.A., spontaneous activity. (N=6, F=17.4, df=4,25, P<0.01.)

activated more by touch when the tactile stimulus was out of sight (rather than in sight). The remaining 9 neurones (28.1%) gave an equivalent response to the tactile stimulus when it was both in and out of sight of the monkey. No cells showed a preference for touch in sight over touch out of sight. So, the majority of cells displayed an inhibition of the somatosensory response when visual cues about the tactile stimulus were available, i.e. when the stimulus could be expected.

Figure 4.8A illustrates this for a touch-sensitive cell (F123A) with passive tactile stimulation of the monkey's hand. The cell's response to touch out of sight (unexpected touch) was significantly greater ($p<0.01$) than the response to touch in sight (expected touch). Touch in sight did not significantly affect the cell's response. A small visual response was observed (clinically) which suggests that the lack of response to touch in sight was not due to incidental visual inhibition of the response but to an interaction between the sight of the tactile stimulus and the tactile stimulus itself. One explanation of this would be that the stimulus is now 'expected'.

A comparable response to that for passive touch out of sight was noted with active touch for cell F123B. Figure 4.8B demonstrates that the monkey actively touching an unexpected object (out of sight) again produced a significantly larger response ($p<0.01$) than the monkey actively touching an expected object (in sight) which also affected the cell's response by significantly increasing its firing rate ($p<0.01$).

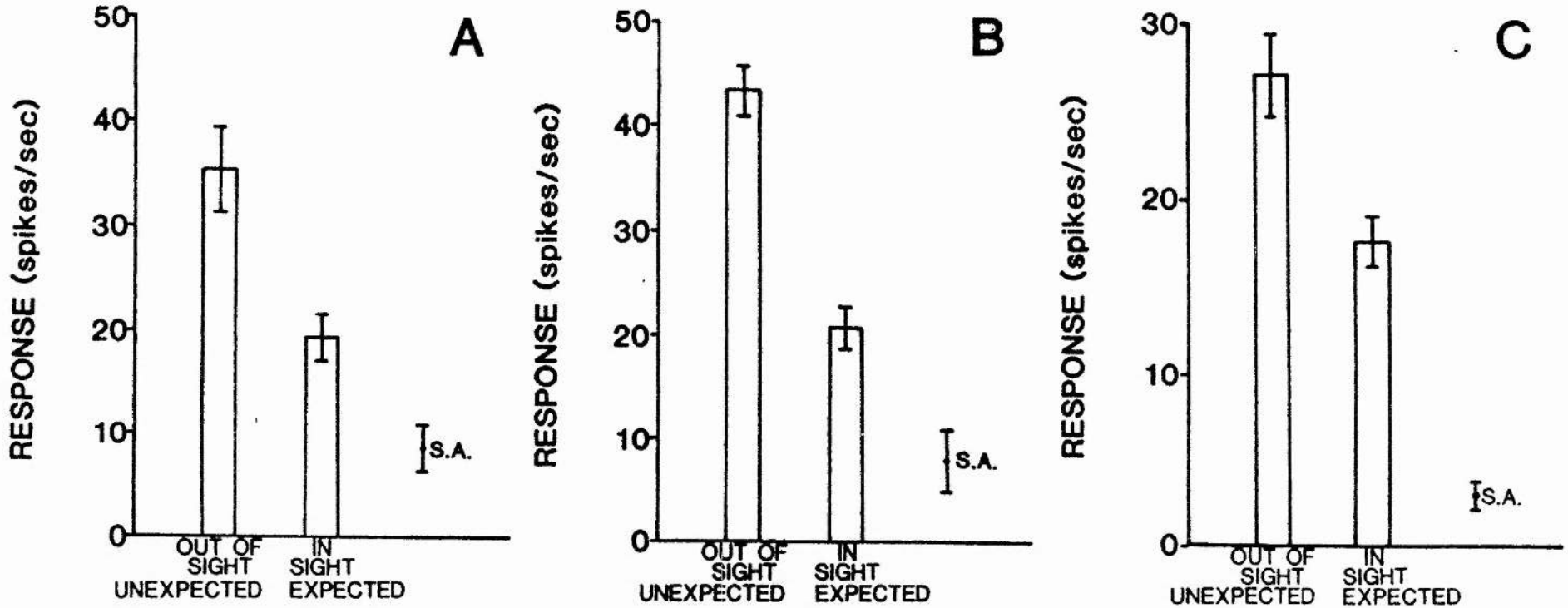


Figure 4.8 Effect of the sight of the (expected) tactile stimulus on the activity of three somatosensory cells sensitive to (unexpected) tactile stimulation out of sight of the monkey. A, cell F123A responsive to passive touch (N=10, F=78.7, df=2,17, P<0.01); B, cell F123B responsive to active touch (N=10, F=599.0, df=2,17, P<0.01); and C, cell F056 responsive to passive detouch (N=10, F=50.5, df=2,18, P<0.01). S.A., spontaneous activity.

The same selectivity for passive unexpected tactile stimulation was observed for a detouch-sensitive cell (F056); i.e. detouch out of sight elicited a significantly greater response ($p<0.01$) than detouch in sight (Figure 4.8C) although detouch in sight did significantly increase the cell's firing rate ($p<0.01$).

4.3.6 Associated visual responses

Of the population of neurones with somatosensory properties being investigated, just over half of these (102/197, 51.8%) also displayed sensitivity to visual stimuli. This proportion of cells is probably an underestimate of the number of cells with a visual response as it is possible that some cells simply were not tested with the appropriate visual stimulus.

Sensitivity to both form and motion of the visual stimulus was investigated in these cells although the visual basis of this sensitivity was not investigated as fully as those cells in Chapter 6. The visual responses were unclassified for 15 neurones (out of 102, 14.7%), i.e. the specific feature (e.g. form or direction of motion) of the visual stimulus that caused the cell to discharge optimally was not identified. An inhibition of the cells' firing rate to any visual stimulus was observed in 3 of these neurones. As the cells were concerned more with the dynamic nature of the stimulus than with its form, the remaining neurones were grouped into the following two classes: (a) directionally non-selective neurones; and (b) directionally-selective neurones (see Table 3). Sensitivity to form

Table 3 Selectivity for motion in visual-sensitive somatosensory neurones of the superior temporal sulcus

Categories of motion sensitivity			Number of cells
I	Directionally non-selective		12
II	Directionally selective		72
	Movement		
	Along z axis	loom	40
		retreat	17
	y axis	up/down	8
		up	7
		down	1
	x axis	left/right	2
		left	2
		right	0
	Appear		4
	Disappear		1

is considered separately for clarity and to simplify classification; for a full understanding of STS cell properties conjoint consideration of form and motion sensitivity is necessary.

(i) Motion sensitivity

(a) Directionally non-selective neurones

Twelve neurones were identified that responded to a visual stimulus moving anywhere in the monkey's visual field. For these cells, the direction of movement of the stimulus was not important, i.e. they did not differentiate between the different directions of movement. In addition, none of the cells differentiated between different shapes of the moving stimuli, i.e. they were not form-specific. Testing of motion sensitivity (usually performed within the monkey's immediate extrapersonal space) at a greater distance from the monkey (1-3 metres) indicated the possibility of a qualitative change in the visual sensitivity of these cells. Eight cells that were observed to have direction-selective responses close to the monkey were reported to have a more general motion sensitivity at a distance from the monkey, i.e. here, they did not discriminate between all directions of movement.

(b) Directionally selective neurones

A large proportion (72/102, 70.6%) of the somatosensory cells with visual responses were activated by movement of a visual stimulus along one of three orthogonal axes centred on the monkey: Up/down (y axis); left/right (x axis); and towards/away (z axis) from the monkey's eyes (Figure 4.9). Cells responded to a single preferred direction giving

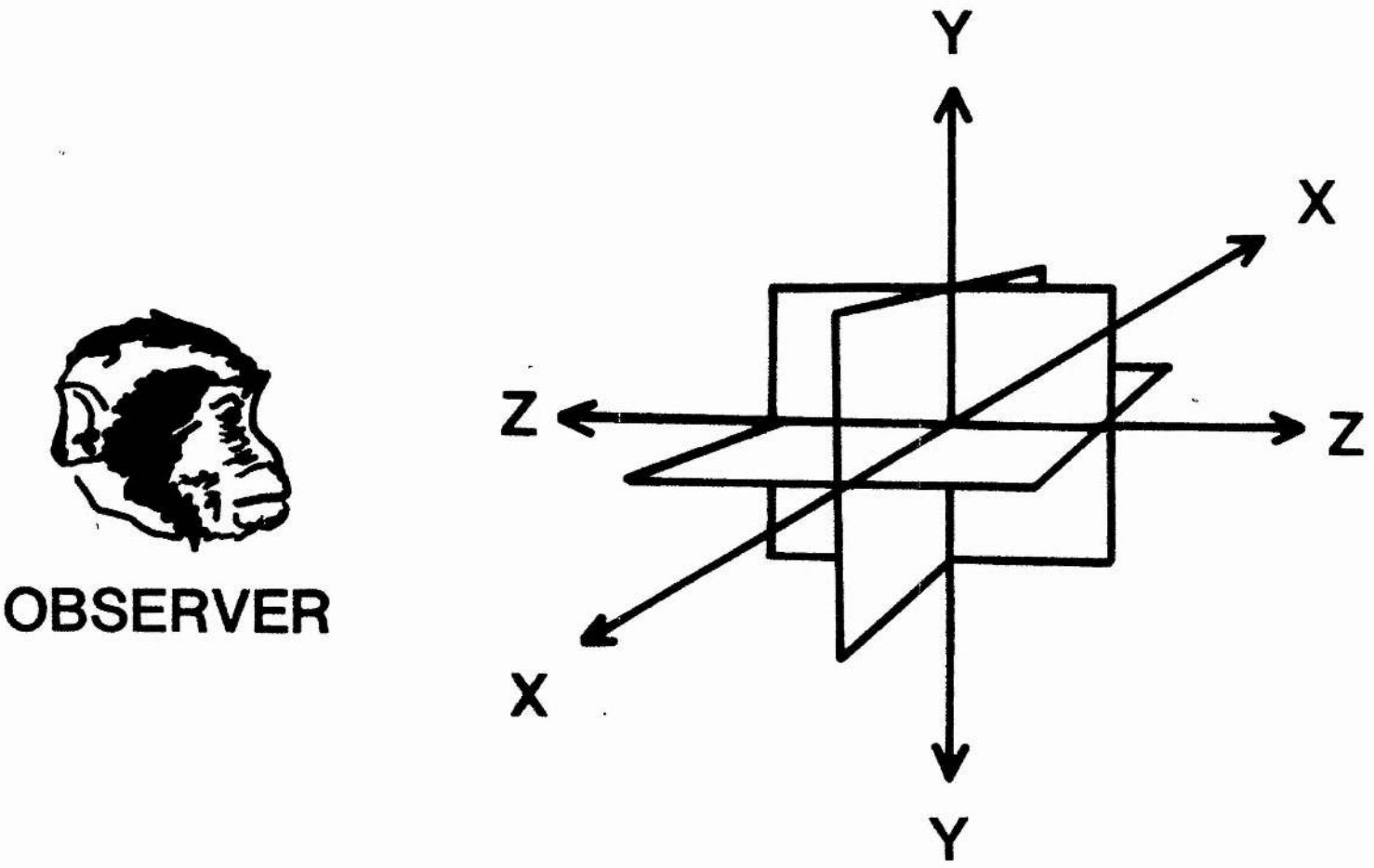


Figure 4.9 Coordinate axes representing the directions of movement which activate somatosensory neurones with associated visual responses. The three Cartesian axes are illustrated relative to the position of the observing monkey. X, left-right axis; Y, up-down axis; Z, towards-away axis.

no response or a reduced response to movements in opposite or intermediate directions. The proportion of cells responsive to a particular direction of motion are indicated in Table 3.

Of these directionally selective neurones, just over half (40/72, 55.5%) preferred the movement of a stimulus (along the z axis) towards the monkey or alternatively, towards the tactile receptive field, as most cells' receptive field included the monkey's whole body surface (see 4.3.4). Two forms of response were typically observed in cells selective for this looming movement; they are illustrated by touch-sensitive cells F068 and F034 in Figure 4.10A and B respectively. Both these cells preferred the movement of a stimulus towards the monkey when compared with other orthogonal directions of movement; namely, movement to the monkey's left or right or directly away from the monkey.

For F068 (Figure 4.10A) the response to a movement directly towards the monkey was significantly greater ($p<0.05$ each comparison) than the responses to other movements. For F034 (Figure 4.10B) a tuning response to movements toward the monkey was observed. Responses to movement directly towards the monkey and to intermediate forward movements (directed forward diagonally 45 degrees from the monkey) were significantly greater ($p<0.01$ each comparison) than the responses elicited by the other directions of movement. These intermediate looming movements, although not on a direct 'hit-course' with the monkey, do possess a forward vector component. Clinical observations suggested that a finer directional tuning was present for 3 (of the 40) 'loom' cells (whose receptive field excluded the face) where

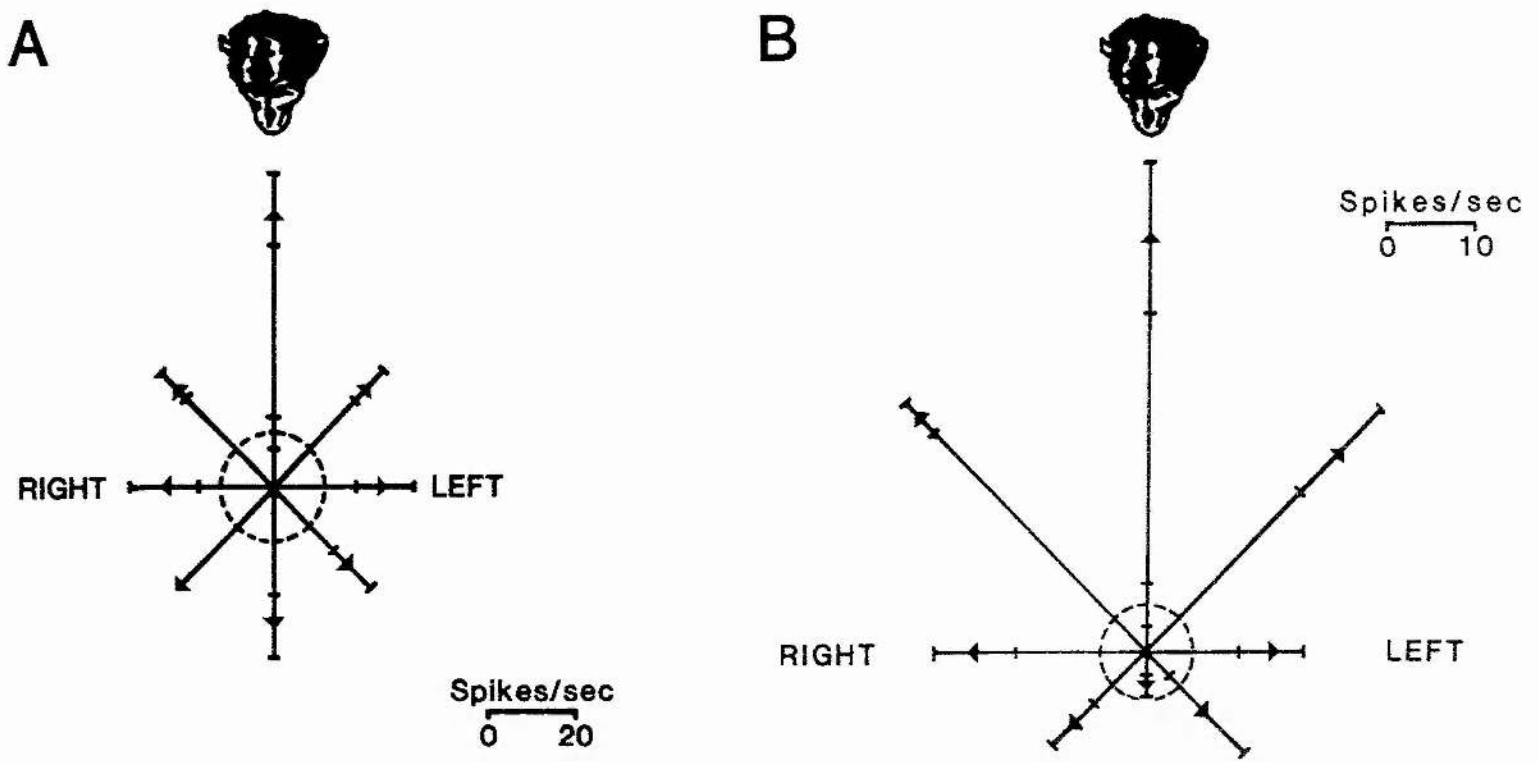


Figure 4.10 Sensitivity to movement of a visual stimulus towards the monkey's receptive field in two touch-sensitive cells. Directions are specified with reference to the monkey's head. Each solid line represents the mean and standard error of response to movement in the direction of the arrowhead. The magnitude of the mean response is given by the length of the line from the intersection point to the arrowhead. The dashed line gives spontaneous activity of the cell with error bars on the vertical line above the intersection point. A, the cell F068 responds most to a movement directly towards the monkey (N[clockwise from top;S.A.]=2,4,4,2,4,2,4,4,4, F=3.3, df=8,21, P<0.02). B, the cell F034 responds equivalently to movements directly towards the monkey and forward movements angled 45 degrees from the monkey (N=5, F=16.1, df=8,32, P<0.01).

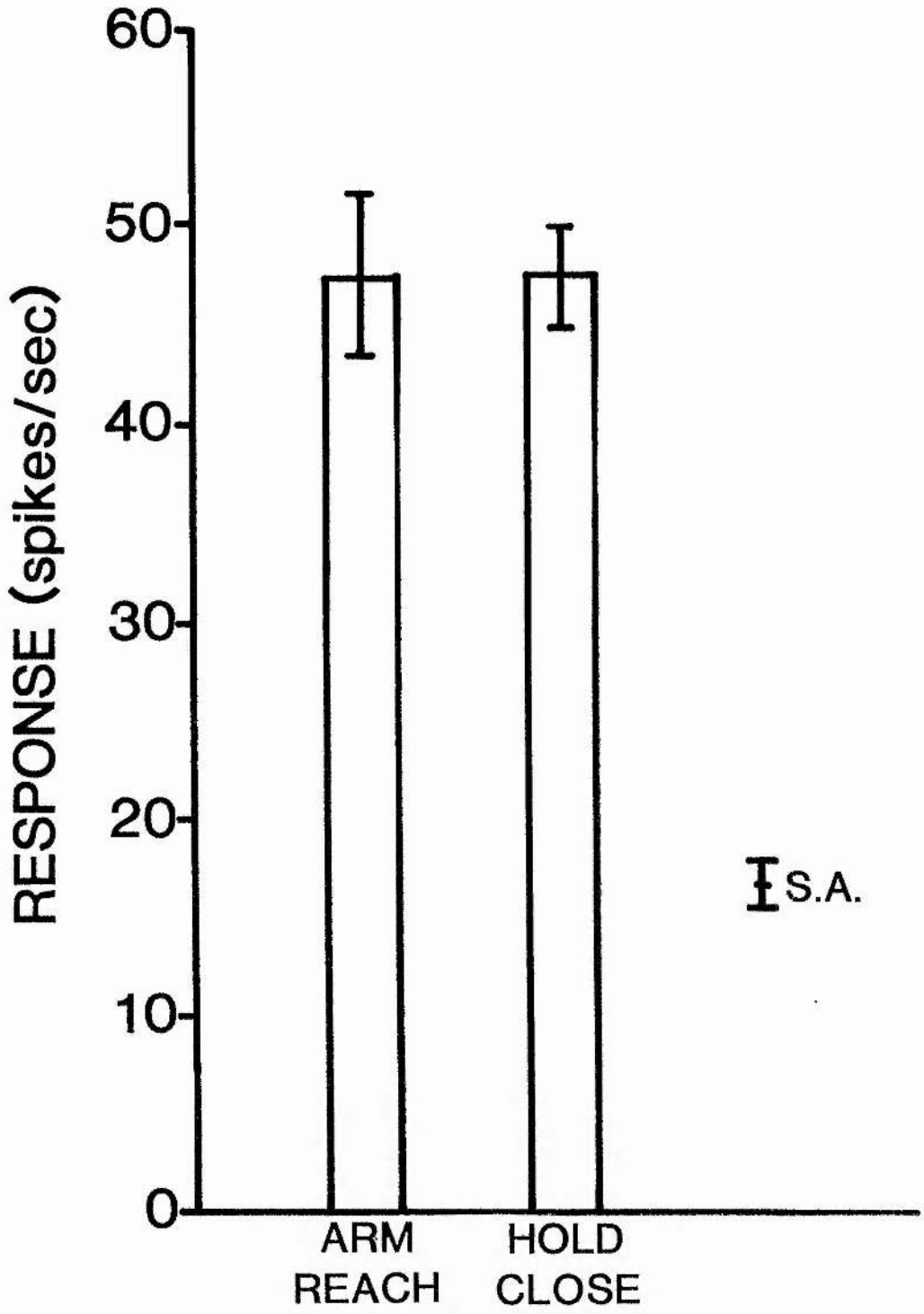


Figure 4.11 Activity of one touch-sensitive cell (F026A) to both a stimulus moving towards the monkey and a stimulus being held close to the somatosensory receptive field. S.A., spontaneous activity. (N=7, F=22.5, df=2,12, P<0.01.)

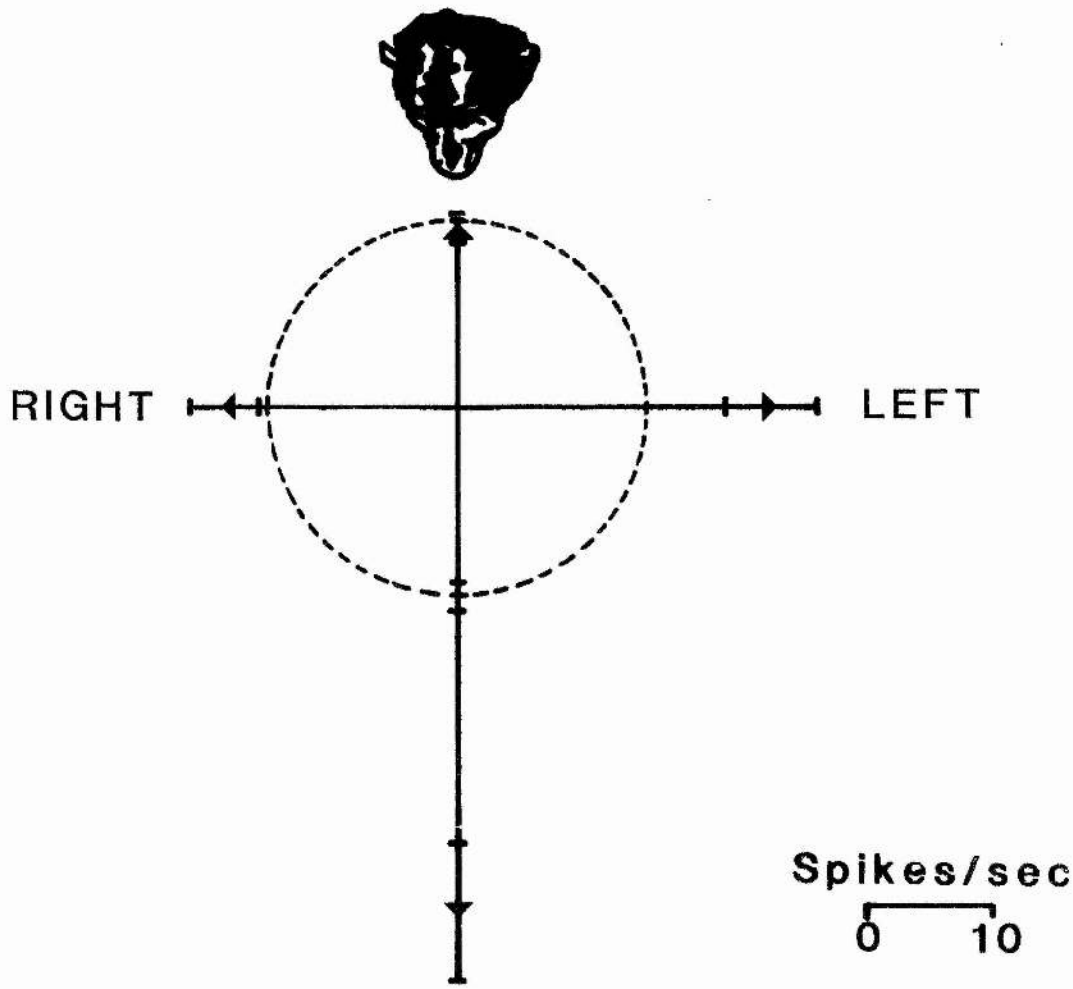


Figure 4.12 Sensitivity to movement of a visual stimulus away from the monkey's receptive field in a detouch-sensitive cell, F093. Explanation of the figure's construction is given in Figure 4.10. (N=10, F=8.7, df=4,36, P<0.01.)

reaching towards the monkey's lower torso elicited a larger response than reaching to the monkey's face.

Two loom cells were additionally sensitive to movement in another direction, one to a stimulus moving up and one to a stimulus moving to the monkey's right. Five neurones responded to an object being held close to the tactile field (within 0.1m) in addition to a movement towards it. Such a response is shown by cell F026 in Figure 4.11 where both a reaching movement towards the monkey (of any stimulus) and the stimulus being held close to the monkey elicit a significant response ($p<0.01$). These responses do not differ significantly from one another.

A smaller proportion (17/72, 23.6%) of the directionally selective neurones were selectively responsive to a movement (along the z axis) away from the monkey (or tactile field). Figure 4.12 demonstrates this sensitivity in a detouch-sensitive cell, F094, for a moving object. Direct movement away from the monkey elicited a significantly greater response ($p<0.01$) than movement in other directions, i.e. movement towards the monkey or to the monkey's left or right. Four cells, in addition to this 'retreat' response, responded to an object disappearing within or from the monkey's visual field. One cell was additionally sensitive to a movement down, low in the monkey's visual field.

An interesting feature of the directionally selective cells so far described, is that the relative proportion of loom or retreat responses differed significantly ($p<0.01$) with the touch- or

detouch-sensitive cells (two way chi-square test of association, 1 df, observed x = 63.65). All the 'loom' visual responses were observed in touch-sensitive cells and all the 'retreat' visual responses in detouch-sensitive cells. None of the touch-sensitive cells had a preferred direction of movement directly away from the monkey and vice versa, none of the detouch sensitive cells had a preferred direction of movement towards the monkey. The behavioural significance of this observation is discussed in section 4.4.

A small group of cells (8/72, 11.1%) showed a preference for movement along the y axis; 7 cells responding to a stimulus moving up and 1 cell to a stimulus moving down in the monkey's visual field. Figure 4.13 illustrates the directional sensitivity of a cell (F114) sensitive to movement up in the monkey's visual field. In the horizontal plane (Figure 4.13A) the cell responded more to movement directly and diagonally up (45 degrees up from a line perpendicular to the upward direction of motion) than to any other movements ($p<0.01$ each comparison). Typical directional tuning was observed where responses to movements at 45 degrees to the preferred upward direction of motion were reduced ($p<0.01$ for a movement up 45 degrees to the monkey's right, and $p<0.05$ for a movement up 45 degrees to the monkey's left) compared with the response to movement directly up. Responses to movements 90-180 degrees from the preferred direction did not differ significantly from the cell's spontaneous activity.

In the vertical plane (Figure 4.13B) the cell's responses to a movement directly up and 45 degrees (forward) to the preferred direction were significantly greater than all the other directions of

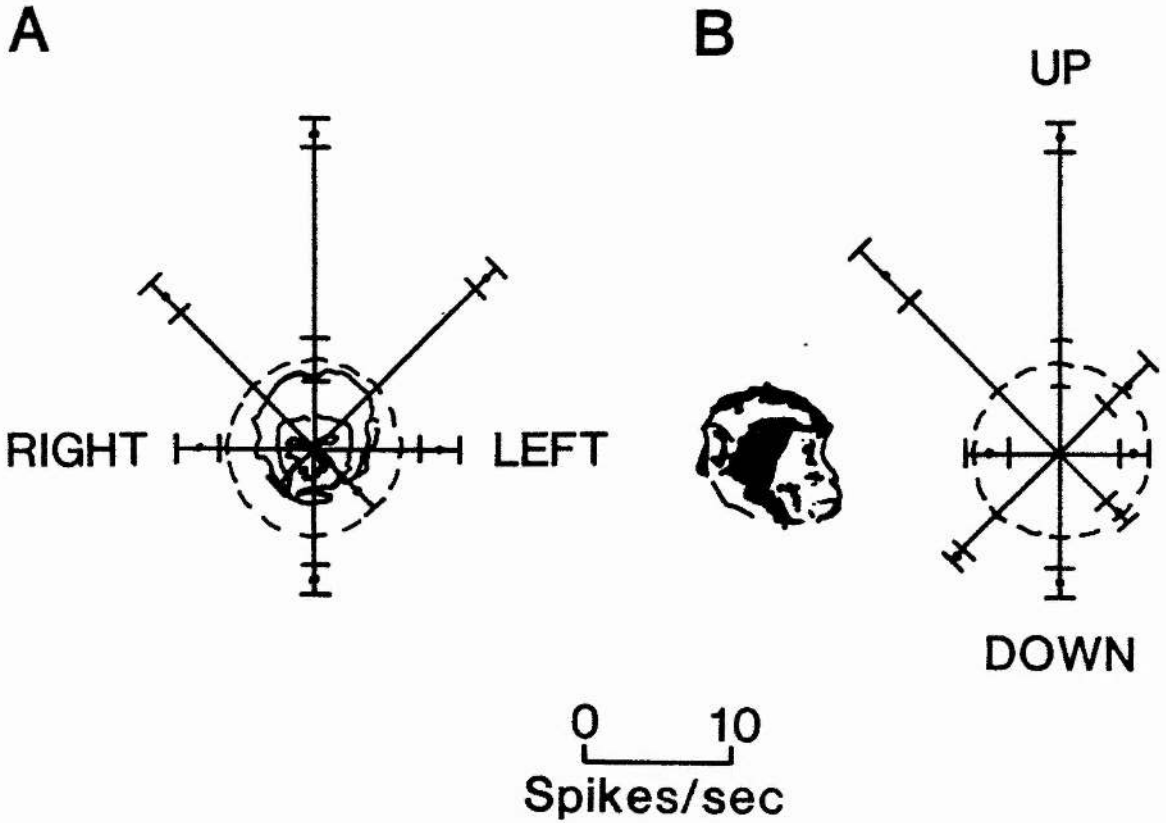


Figure 4.13 Sensitivity to a visual stimulus moving up in the monkey's visual field, for a touch-sensitive cell, F114. A, a tuning response to visual movements up in the horizontal plane (N=5, F=20.6, df=8,32, P<0.01); B, a tuning response to visual movements up in the vertical plane (N=5, F=17.9, df=8,32, P<0.01). Directions of movement (up/down, left/right) are indicated with respect to the viewing monkey; otherwise the legend is as for Figure 4.10.

motion ($p<0.01$ each comparison) which were within the range of the cell's spontaneous activity.

The remaining directionally selective neurones, composed two cells that were selective for a stimulus moving along the x axis, both responsive only to movement to the monkey's left; and five cells that responded transiently to stimuli moving into or out of view of the monkey. Of the latter, 4 cells preferred central or peripheral movement into view (appear) and 1 cell preferred movement out of view (disappear).

(ii) Form sensitivity

The majority of the visual responses (88/102, 86.3%) were form insensitive, but for 14 out of the 102 cells tested (13.7%) form sensitivity was evident. Eleven of these were found to be selective for particular movements of a body (or body part) but were unresponsive to other 3-dimensional stimuli. Figure 4.14 depicts a cell (F123) sensitive to the form of the stimulus moving towards the monkey, in that the cell prefers arms (to equivalent sized bars) reaching in this way ($p<0.01$). The cell also demonstrates a preference for bimanual arm reaching over unimanual reaching ($p<0.01$). Neither bimanual bar reach or unimanual arm reach produced a significant response. In contrast F026 (in Figure 4.15) responds to both an arm and a bar reaching towards the monkey ($p<0.01$ each comparison). For this form-insensitive cell there is no significant difference between the reaching movement made by either an arm or a bar.

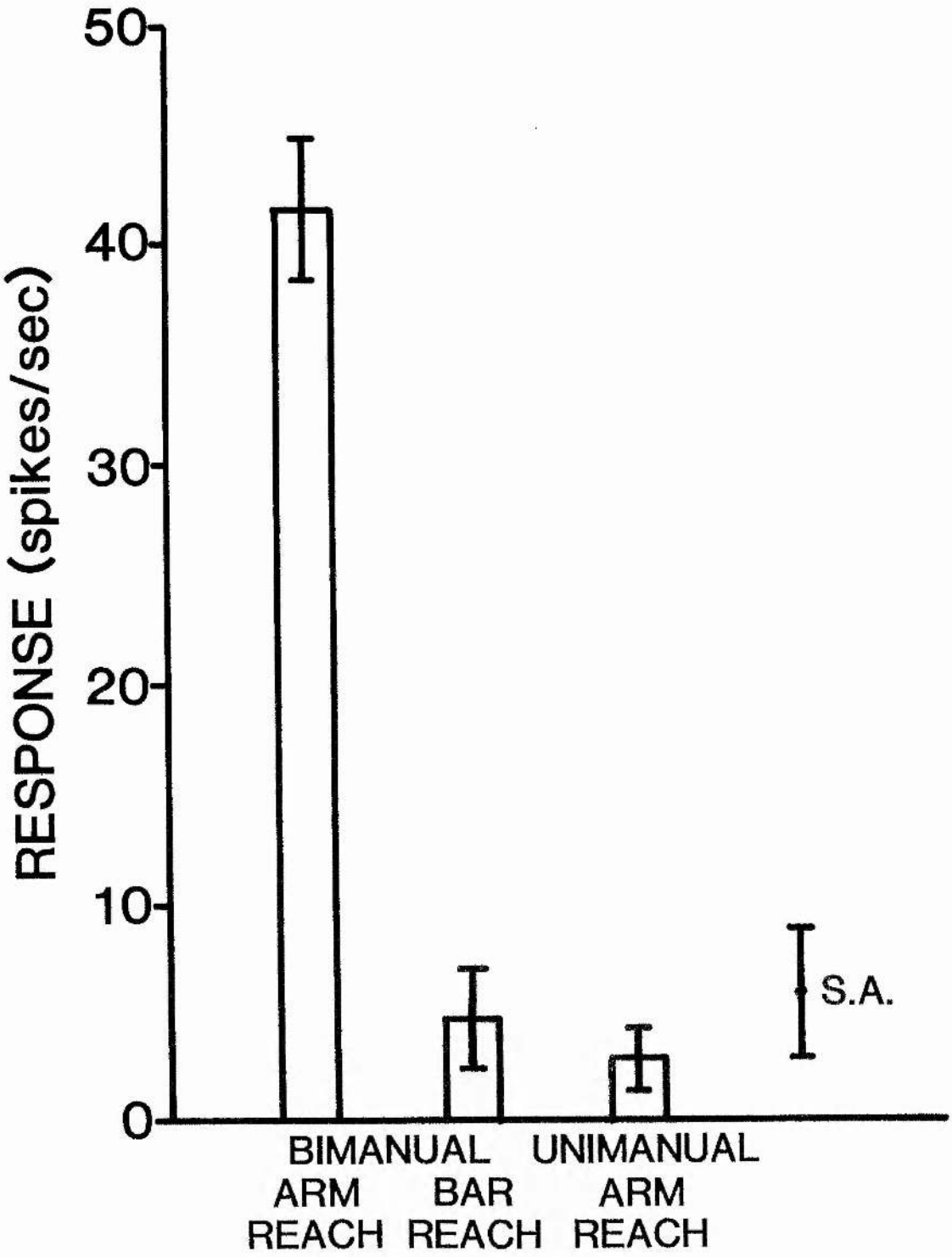


Figure 4.14 Sensitivity to the form of the visual stimulus in a touch-sensitive cell, F123C. The cell is more responsive to two arms reaching toward the somatosensory receptive field than two bars of equivalent size (or one arm) moving in the same way. S.A., spontaneous activity. (N=5, F=24.0, df=3,12, P<0.01.)

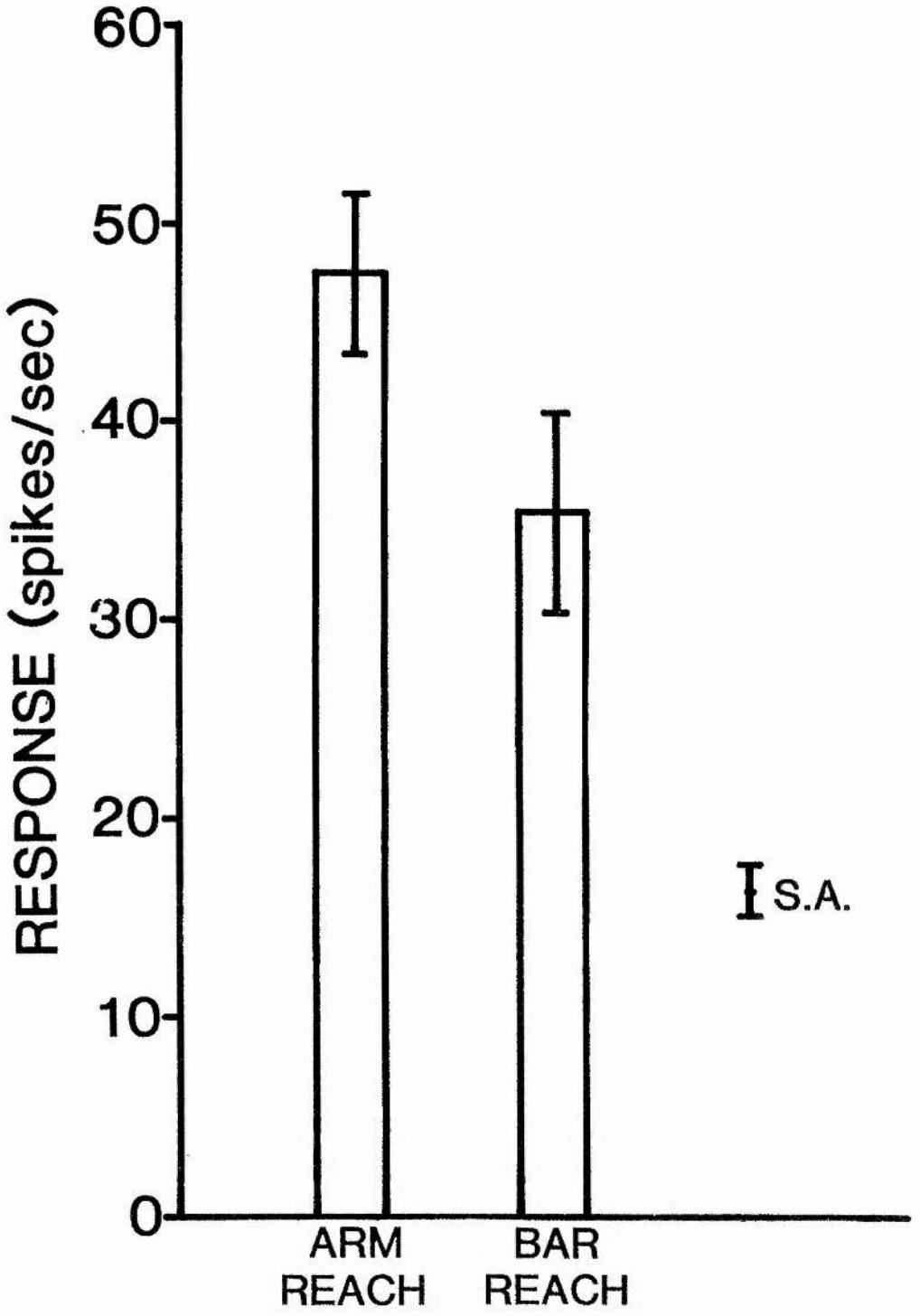


Figure 4.15 Response of one touch-sensitive cell (F026B) to a visual reaching movement towards the somatosensory receptive field that is unaffected by the form of the stimulus. S.A., spontaneous activity. (N=7, F=17.4, df=2,12, P<0.01.)

Within the motion-sensitive cell categories 5 loom, 2 retreat and 4 up-sensitive cells were form selective. All five of the form sensitive 'loom' cells and 2 up-sensitive cells preferred the appropriate movement of an experimenter's limb to that of the whole body; three of the loom-sensitive cells showed a preference for bimanual rather than unimanual reaching as shown in Figure 4.14. The two form-sensitive cells selective for a retreat movement preferred whole bodies to limbs or other 3-dimensional objects moving away from the monkey. The remaining cells were selective for a movement up. The two remaining up-sensitive cells responded selectively to the head of an experimenter rotating up from a head down view to full face and from full face to a head up view (see Perrett et al, 1984, 1985b for a more detailed description of this type of visual sensitivity).

Three cells responded to specific static visual stimuli (e.g. face views) but they will not be reported here as this type of visual response has been described in more detail in Chapter 6.

4.4 Discussion

Three types of somatosensory cortical neurones in the upper bank of the STS (superior temporal sulcus) are described. The first and largest group consists of cells with cutaneous input, sensitive to the onset and/or offset of tactile stimulation. The second group consists of cells sensitive to joint movement and the third group, of cells sensitive to vibration. None of these neurones were influenced by

simple stimulus parameters such as the size, shape or texture of the tactile stimulus; the remarkable feature of these cells being their responsiveness to unexpected, rather than expected, tactile stimuli.

4.4.1 Somatosensory responses in light of previous work

No previous detailed investigations of the somatosensory properties of cells in the STS, in awake, behaving monkeys, has been carried out. Indeed the only study of such cells in this area of the brain was made by Bruce, Desimone and Gross (1981) in anaesthetized and immobilized monkeys. It will therefore be of interest to compare the general findings of the present study with the preceding work of Bruce et al.

The area of the brain investigated by Bruce et al although termed STP (superior temporal polysensory area) was defined as the upper (or dorsal) bank and fundus of the anterior portion of the superior temporal sulcus which is equivalent to the area of cortex (termed STS) in this study. The main focus of Bruce et al's investigation was on the visual properties of the neurones in the STS, and incidental to this was the report that 17% of the cells responded to visual and somaesthetic stimuli. They recount that 'with one exception, no cell responded to ... somaesthetic stimuli in the absence of a visual response'. For the bimodal cells, therefore, they describe the somaesthetic receptive fields as large and bilateral, generally including the entire body surface, and they state that usually any type of stimulus (light/deep touch, stroking, blowing) would elicit a response. (The median latency of the somaesthetic responses was

55ms.)

Considering the data from the present study, 18.1% of the cells responded to somatosensory stimuli; 50% of these cells exhibiting a bimodal response (to both somatosensory and visual stimuli). This contrasts with Bruce et al's report of a complete absence of unimodal somaesthetic cells. One explanation might be that in the present study the number of cells with a visual response was underestimated as this modality was not as systematically studied as the somatosensory. With regard to the size of the somatosensory or somaesthetic cells' receptive field, the response of these cells to different types of stimuli and their latency to respond, the present data replicates the findings of Bruce et al.

However, as Bruce et al did not make a systematic study of the somaesthetic responses they observed , they failed to identify perhaps the most interesting property of these somatosensory cells - their ability to discriminate between expected and unexpected tactile stimuli through the somaesthetic modality alone, and by integrating information from both the visual and somaesthetic modalities. Although Bruce et al reported that visually responsive neurones gave excitatory or inhibitory responses to visual stimuli, no mention was made of a visual-somatosensory interaction where a visual stimulus could inhibit a somatosensory response.

Bruce et al meticulously reported the visual responses of the neurones in STP and they observed that nearly all neurones preferred moving to static stimuli. Of these cells in the present study with a visual

response, a similar observation was made; a small number of cells were selective for static stimuli but the majority preferred a moving stimulus. A number of cells demonstrated direction selectivity responding to some directions of movement more strongly than others.

The general classes of movement these cells responded to were equivalent to those in the present study, i.e. movement in depth (z axes) and in the fronto-parallel plane. No correlation, however, between the direction sensitivity of the visual response and the form of the somatosensory response was indicated by Bruce et al: "Neurones sensitive to one, two, or three modalities were distributed similarly among all classes of direction sensitivity". As Bruce et al did not report a discrimination between the ON, OFF and ON-OFF forms of somatosensory response it is unlikely that they would have seen the association between a movement (in depth) towards the monkey, and touch; and a movement away from the monkey, and detouch, observed in the present study. (N.B. ON, OFF, ON-OFF responses have been reported in the STS for auditory stimuli (Benevento et al, 1977).

Thus, in conclusion, the present study contradicts little in Bruce et al's report of the somaesthetic response properties of cells in the STS (or STP); but it does bring to light some additional properties of the cells which are essential to understand, if we are to have a comprehensive knowledge of the functions of the STS.

4.4.2. Expected/unexpected dimension of tactile stimulation

(a) A unique response?

Mackay and Crammond (1987) rightly point out that "the attribution of neuronal discharge to an internal phenomenon such as expectation is impossible to prove, because the phenomenon can't be strictly measured or controlled". Nevertheless evidence presented in this chapter does point to the presence in the STS of cells responsive to unexpected but not exptected tactile stimuli, and hence of input providing predictive information about immediately impending events of importance to the monkey.

The phenomenon of expectation or anticipatory activity is not unique in itself. Mackay and Crammond (1987) have reported single units in posterior parietal cortex showing anticipatory types of activity, i.e. changes in cells' discharge rates prior to an event. There are indications of similar changes in activity in parts of premotor, prefrontal, frontal, cingular cortex, frontal eye fields, primary motor cortex and brainstem (e.g. Mauritz and Wise, 1986; Niki and Watanabe, 1979; Bruce and Goldberg, 1985; Lamour et al, 1980; Bakay-Pragay et al, 1978). To some extent the responses reported in the present study to the expected/unexpected dimension of touch are unique - in that they ignore the source of the stimulation (self or external) and have their effect not prior to the event but at the time of the event.

It is only with Evarts (1966) innovative techniques for recording in awake, behaving monkeys that such activity could have been identified. As prior to this, observations of tactile stimulation as a result of the monkey's own movements (active touch) were not possible. Most

testing for the somatosensory properties of cells is with the subject unable to see the tactile stimulus where by definition (from 4.2.2) an unexpected greater than expected difference can only be seen with active touch. Under such conditions it would be impossible to observe (or even test) a cell's response sensitivity to an expected or unexpected tactile stimulus.

Where active touch could be explored, still no expected/unexpected differences as such have been noted. Although, in contrast to the present study's data, differences between active and passive touch have been observed (Iwamura et al, 1985; Leinonen et al, 1979; Mountcastle et al, 1975). Notably, responses during active somatosensory stimulation were usually greater than responses to passive stimulation of an equivalent nature. In the present study though, expected/unexpected differences were observed for both active and passive conditions.

Hence within the definitions given for the present work the phenomena reported here are unique. This is bearing in mind that it's impossible to determine from methodological details of others' work the extent to which the expected/unexpected dimension of touch has been truly explored.

(b) Theoretical importance

Why should an animal need to perceive or comprehend whether a stimulus is expected or unexpected and how sophisticated is the sensory analysis that might support such a decision? Perhaps the best way to address this question initially is to consider a situation that any of

us might find ourselves in. Imagine you have just boarded a busy underground train (where all the seats are occupied) and are required to move down the carriage aisles to make room for other passengers alighting the train. Moving down the aisle you negotiate fellow travellers, perhaps brushing against them in your effort to pass them, or gently guiding them out of your way as you pass. Touching these people necessitates no response or reaction on your behalf and concentrating on your directive (of trying to reach a place to stand comfortably in the carriage, perhaps) you are probably not even 'aware' of these social actions.

These tactile encounters are expected since: (1) you are initiating the movement that will result in tactile stimulation, the spatial and temporal characteristics of these actions being implicit - i.e. providing no external incidents or agents change the immediate environment (for example the train violently lurching causing the standing passengers to bump into one another), making a prediction of when and where the actual tactile encounter will occur is feasible; and (2) visual cues concerning the environment allow you to predict the nature of the tactile surface to be contacted with some degree of accuracy.

In an alternative situation, suppose you are making your way down the aisle of the busy train carriage and a passenger travelling behind you firmly places their hand on your body. Assuming the noise of the train masked their approach and because they came from behind you, the tactile stimulation would be unexpected. An immediate decision must be made about the action to be taken to this stimulus. The initial

response might be to turn around and survey the owner of the hand, to remove it from your body, or to move away from this passenger. You are not to know if, for instance, the person simply wished to pass you or if the tactile contact had sexual intent. Introspectively there is an immediate and compelling 'sensation' of being touched and of the tactile sensation being unexpected. In fact, we anticipate (subconsciously) virtually every act to the extent that unanticipated (or unexpected) events are startling experiences.

The point being made here is that any unexpected stimulus requires a decision on whether a response to the stimulus is necessary or not. The situation is analogous to the 'flight or fight' paradigm; on encountering an unexpected stimulus the first decision made is whether to face up to the situation (fight) or whether to flee (flight). Further analysis of the stimulus itself is of secondary importance.

With the example above the behavioural significance of having representations of expected and unexpected categories of stimuli becomes clearer if these representations are used to determine the appropriate social or emotional response to a stimulus. Discriminating between expected and unexpected tactile stimuli appears to serve a purpose in humans, but is this purpose ecologically valid in monkeys? Illustrations of a monkey's interaction with a conspecific or a predator may clarify this question. In the first situation consider a monkey (A) grooming the back of a monkey (B) in a social colony. Suppose another monkey (C) approaches this couple from behind, perhaps with the intent of grooming B. Should C brush against or intentionally touch A, an immediate social response must be

affected by A. Monkey A is not to know C's intentions so must determine what action to take; to appease monkey C if monkey A is submissive or threat monkey C if monkey A is dominant. Whatever the outcome, the unexpected tactile encounter initiated by monkey C requires a response unlike the self-initiated expected tactile feedback which results from monkey A grooming B. Likewise, if monkey B was facing and grooming monkey A, touch would be expected as A could see the approaching stimulus (monkey B's hand/s) and predict the tactile 'collisions'.

An alternative situation might be a monkey negotiating jungle terrain by swinging from branch to branch. From experience the monkey would have some knowledge of the tactile nature of the surfaces to be contacted and with visual feedback to determine the temporal characteristics of these encounters, these tactile experiences (both touching and removing touch from the branches) would be expected. However, by introducing a predator into this situation the tactile information received by the monkey could be completely different. Suppose a well camouflaged snake spanned the length of one branch to be used as a hand-hold for the monkey. With the snake's camouflage rendering it indistinct from its background the monkey would have no prior visual warning of its presence; thus, happening upon the snake as opposed to foliage would relay to the monkey unexpected tactile information. In all probability the monkey would be forced to alter its behaviour, acknowledge the predator's presence and react accordingly (retract its hand, scream, etc.).

It is hoped that this lengthy account of the nature and behavioural

consequences of unexpected tactile stimulation purveys the obvious importance of the expected/unexpected dimension of touch and amplifies how pervasive this dimension can be. As Mauritz and Wise (1986) expanded, "the ability to predict events and react to them more efficaciously thereby, may represent a significant advantage to an animal".

Numerous situations must exist where spatial, visual and somatosensory information of a monkey's immediate extrapersonal space or grasping space (Grusser, 1983) render objects (or stimuli) expected. It is only an unexpected change in this 'local' environment that must be coded to enable the monkey to respond with a socially or emotionally appropriate response and to allow an update of the internal representation of the monkey's extrapersonal space such that the unexpected stimulus can become expected.

(c) How does a stimulus become expected?

These examples illustrate how complex the system for determining whether a stimulus is expected or unexpected must be; not only is the property of expectedness context-dependent, but it also relies on sophisticated integration and association of different modalities and functions. Obviously one question that urges speculation is: When and how does an unexpected stimulus become expected? The present research cannot shed much light on this problem although the results should dispell any ideas that habituation of the somatosensory response alone is the mechanism by which a stimulus is no longer unexpected. Even with repeated stimulation (up to 50 trials) of the monkey's body surface with an unexpected stimulus habituation of a

cell's response was rarely observed.

To determine the expectedness of a stimulus a vast amount of information from several functionally distinct systems would need to be integrated: Sensory information - both visual and somatosensory cues about the nature of an object; motor information - the motor movement necessary to contact an object in space (for self-initiated tactile stimulation); and memorized spatial information - the location of an object in space. Thus, habituation of a cell simply to sensory input cannot explain this mechanism. (For touch expected through the visual modality a possible explanation is given in 4.4.3.)

This complex integration of information required to determine the expectedness of a stimulus does suggest that the STS is functioning at a high level of processing in the somatosensory modality, just as this has been suggested for the STS in the auditory modality (Benevento et al, 1977) and the visual modality (e.g. Perrett et al, 1984, 1985a,b).

4.4.3 Associated visual responses

A population of the cells in the STS responded independently of their somatosensory response to visual stimuli. Within this population a significant association was observed between touch-sensitive cells and visual sensitivity to a movement towards the tactile receptive field (loom), and detouch-sensitive cells and visual sensitivity to a movement away from the tactile receptive field (retreat). In an

effort to explain this relationship between the cells' somatosensory and visual sensitivities the primary step is to try and analyse the information about the world both modalities are providing the cell.

With an object moving towards the monkey (i.e. on a hit-course with it) there is a greater probability that this will result in the monkey being touched. Conversely, with a movement away from the monkey there is less probability of the monkey being touched; this movement could even be indicative of or follow the removal of touch (detouch). So, the loom/retreat visual responses may give an indication of the likelihood of change in tactile stimulation. This would be a useful function of the cells but it does not explain why these visual responses are associated with the particular somatosensory properties in the same cells.

The second step to take in order to determine the usefulness of this relationship is to examine the responses that the bimodal information would evoke. Both the looming movement of an object and being touched might elicit the same response, that of moving away from the stimulus (an escape response). In the same way, a retreating object and the removal of touch might elicit the same form of response; the information here could imply that the monkey need not elicit an escape response or needs to follow the retreating stimulus. What is important to stress here is that it is the behavioural significance of the actions - touch and loom, and detouch and retreat - that is equivalent. In this capacity the STS appears to be involved in providing a high order somatosensory-visual analysis to mechanisms for assigning an appropriate response to specific stimuli, as has been

assigning an appropriate response to specific stimuli, as has been suggested for unexpected tactile stimuli (4.4.2) and even for faces (Chapter 7).

An interesting feature of these bimodal cells is the possibility that each modality response may play an independent role in addition to its associated role in governing the behaviour of the animal. Such an independent role may arise in determining the expectedness of a stimulus when tactile stimulation is in sight of the monkey (i.e. with visual information about the tactile stimulus available). This independent role may be seen to have a feed forward effect on other purely tactile cells, for example.

Consider one hypothetical scheme for explaining the role of a bimodal cell in conjunction with a unimodal tactile neurone and a visual neurone. (The presence of loom-sensitive cells in this area of cortex in the STS is reported by Perrett et al, 1985a). Supposing an object moving towards the monkey caused excitation of the loom-sensitive cell and the loom component of the bimodal cell. If these neurones then, in turn, were responsible for an inhibition of the touch-sensitive cell and/or the touch component of the bimodal cell, this would effectively reduce the responsiveness of these cells to an expected stimulus. So this could be a mechanism by which a stimulus can be expected through the visual modality for a touch-sensitive cell. An identical scheme could not hold for detouch-sensitive cells with a visual response to an object's retreat as the tactile stimulation precedes the visual action.

4.4.4 Information available for the STS to determine the expectedness of a stimulus

In the previous chapter (3) the cellular properties and functions of areas involved in somatosensory processing were reviewed in conjunction with the anatomical connections between these areas. They were discussed in relation to two parallel tactile processing pathways involved with the tactile discrimination and recogniton of objects and the spatial analysis of objects through the somatosensory and visual modalities. No position in these pathways was considered for the STS mainly because of the scant nature concerning the dimensions of somatosensory processing within this area - and the largely speculative account of its overall functions.

The present study has described cells in the STS whose activity can best be interpreted as discriminating between expected and unexpected tactile stimuli. To understand the response selectivity of these cells it is essential first to consider the information that would be needed to establish such selectivity. It is then helpful to speculate on the potential sources of this information from the functional properties of areas of the somatosensory and association cortex and to assess the plausibility of such areas as routes via which the appropriate information could be made available to the STS. Placing the STS in one or both of the proposed tactile pathways at a level of processing appropriate to the properties of the cells and the function of the STS as a whole should then be possible.

Before judging whether the appropriate information is available to the

STS for deriving the expectedness of a tactile stimulus, it will be useful to recap on the features necessary for this. It is essential to have: (1) sensory information about the nature of the stimulus, i.e. its shape, size and texture; (2) sensory motor feedback to indicate the extent of movements executed and hence the likelihood of encountering objects of remembered spatial positions; (3) associative memories based on sensory experiences from which predictions are set up which may or may not be matched; (4) visual feedback in passive tactile stimulation indicating the proximity of a stimulus to the tactile receptive field; and (5) a spatial representation of the monkey's immediate environment, i.e. the location in space of all objects in the monkey's extrapersonal space (at one moment in time) relative to the monkey's body axis.

These requirements will be considered point by point:-

(1) The SI-SII-insular cortex tactile processing pathway (Mishkin, 1979; Murray and Mishkin, 1984; Murray et al, 1980) attributed with a functional role in tactile discrimination and recognition of objects would seem to be the best route by which neurones in the STS could be supplied with the appropriate information about the sensory nature of the stimulus, e.g. its size, shape, roughness, hardness, etc. There is now anatomical evidence to support this claim, as Friedman et al (1986) have demonstrated a reciprocal connection between the dysgranular fields of the insular cortex and both the upper and lower banks of the STS cortex. Another sensory route for this information may be through area 7 of the posterior parietal association cortex which itself receives projections from both SII and the insular cortex (Friedman et al, 1986).

(2) The sensory motor feedback necessary for STS cells to determine what motor movements would result in tactile collision with a 'known' object in space could arise from the following systems. Numerous studies of neurones in the posterior parietal cortex report high involvement of cells in the active movements of the monkey (see Chapter 3), in particular of visually guided (area 7) and somaesthetically guided (area 5) movements to objects in the monkey's extrapersonal space. Such information from the SI-area 5-area 7 pathway could adequately provide the STS neurones with the appropriate sensory motor feedback, and projections from area 7 (both regions 7a and 7b) do project to the upper bank of the STS (Seltzer and Pandya, 1978, 1984).

(3) Mishkin (1982) postulates that coded representations of objects are stored in the association areas of the cortex whenever stimulus activation of these areas also triggers a cortico-limbo-thalamo-cortical circuit. Once established, he suggests that the stored central representation can enter into association with a variety of other stored representations (sensory, affective, spatial, motor) via reciprocal connections with the relevant structures. Hence the associative memories necessary for defining the expectedness of a stimulus could be established within the STS association cortex by virtue of its reciprocal connections - sensory associations via the insular (tactile) and inferotemporal (visual) cortices, spatial and motor through the posterior parietal cortex, and affective (and crossmodal) associations via the amygdala (see Chapter 3).

(4) Integration between visual and tactile stimulation such that would indicate the proximity of an object (whether stationary or moving) to the tactile receptive field has been reported in the posterior parietal association cortex, predominantly in area 7 neurones. The visual information requisite for the STS cells to derive the expectedness of a tactile stimulus in passive stimulation could therefore emanate once more from the SI-area5-area 7 tactile-visual pathway. As previously described, efferent projections from area 7 to the STS have been reported (e.g. Seltzer and Pandya, 1978, 1984) but whether these projections are for visual, somatosensory or integrated visual-somatosensory information is still unknown.

(5) Finally, the STS cells require information relating to the spatial location of objects in the monkey's immediate environment with reference to the monkey's body axis. Although functions attributed to the posterior parietal cortex as a whole include the formation of a spatial representation of the monkey's body and extrapersonal space, this is primarily for guiding motor acts to targets of interest (e.g. Mountcastle et al, 1975). The physical location of objects in space is more a memory function, perhaps attributable to the amygdala/hippocampal complex with which the STS has direct and indirect connections (e.g. Aggleton et al, 1980).

4.4.5 A place for the STS in tactile processing pathways?

All the observations suggest that in order to perceive objects as

either expected or unexpected, interaction between sensory modalities and the functional integration of a number of systems is essential. It is perhaps only at the level of the STS that this integration is completed such that the dimension of expected/unexpected tactile stimulation can be coded at the cellular level.

This suggests that the STS might function in somatosensory processing at a different level to that of the posterior parietal cortex or the insular cortex, the last cortical stages in the proposed tactile processing pathways (Murray and Mishkin, 1984; Murray et al, 1980). Physiological evidence concerning the increase in receptive field size posteriorly from SI to area 5 to area 7, and from SI to SII to insular cortex, corroborates this view; the present study having revealed that the receptive fields of cells in the STS are larger than those of area 7 or insular cells, including the entire body. It could be proposed therefore that the STS fits into both the tactile pathways as a high order cortical processing stage; and functions in channeling somatosensory information to the limbic structures either subsequent to or in parallel with the insular and parietal routes.

4.5 References

Aggleton, J.P., Burton, M.J., and Passingham, R.E. (1980) Cortical and subcortical afferents to the amygdala of the rhesus monkey (Macaca mulatta). Brain Res. 190:347-368.

Bakay-Pragay, E., Mirsky, A.F., Ray, C.L., Turner, D.F., and Mirsky, C.V. (1978) Neuronal activity in the brain stem reticular formation during performance of a 'go-no go' visual attention task in the monkey. Exp. Neurol. 60:83-95.

Benevento, L.A., Fallon, J.H., Davis, B., and Rezak, M. (1977) Auditory-visual interaction in single cells in the cortex of the superior temporal sulcus and the orbital frontal cortex of the macaque monkey. Exp. Neurol. 57:849-872.

Bruce, D., Desimone, R., and Gross, C.G. (1981) Visual properties of neurones in a polysensory area in superior temporal sulcus of the macaque. J. Neurophysiol. 46:369-384.

Bruce, C.J., and Goldberg, M.E. (1985) Primate frontal eye fields: Single neurons discharging before saccades. J. Neurophysiol. 53:603-635.

Evarts, E.V. (1966) Methods for recording activity of individual neurons in moving animals. In: R.F. Ruhsmer (ed.) Methods in Medical Research, Vol. 11. Year Book Medical Publishers, Chicago, pp. 241-250.

Fetz, E.E. (1981) Neuronal activity associated with conditioned limb movements. In: A.L. Towe and E.S. Lusche (eds) Handbook of Behavioural Neurobiology, Vol. 5. Plenum, New York, pp.493-526.

Friedman, D.P., Murray, E.A., O'Neill, J.B., and Mishkin, M. (1986) Cortical connections of the somatosensory fields of the lateral sulcus of macaques: Evidence for a corticolimbic pathway for touch. J. Comp. Neurol. 252:323-347.

Grusser, O.-J. (1983) Multimodal structure of the extrapersonal space. In: A. Hein and M. Jeannerod (eds) Spatially Oriented Behaviour. Springer Verlag, New York, pp.327-365.

Hyvarinen, J., and Poranen, A. (1974) Function of the parietal associative area 7 as revealed from cellular discharges in alert monkeys. Brain 97:673-692.

Iwamura, Y., Tanaka, M., Sakamoto, M., and Hikosaka, O. (1985) Vertical neuronal arrays in the postcentral gyrus signalling active touch: A receptive field study in the conscious monkey. Exp. Brain Res. 58:412-420.

Jones, E.G., and Burton, H. (1976) Areal differences in the laminar distribution of thalamic afferents in cortical fields of the insular, parietal and temporal regions of primates. J. Neurol. 168:197-248.

Jones, E.G., and Powell, T.P.S. (1969) Connexions of the somatic sensory cortex in the rhesus monkey. I. Ipsilateral cortical connexions. Brain 92:477-502.

Jones, E.G., and Powell, T.P.S. (1970) An anatomical study of converging sensory pathways within the cerebral cortex of the monkey. Brain 93:793-820.

Lamour, Y., Jennings, V., and Solis, H. (1980) Neuronal activity in monkey somatosensory (SI) and motor (MI) cortex related to anticipation of passive displacement and active contractions of the forelimb. Neurosci. Lett. Suppl. 5:S480.

Leinonen, L., Hyvarinen, J., Nyman, G., and Linnankoski, I. (1979) Functional properties of neurons in lateral part of associative area 7 in awake monkey. Exp. Brain Res. 34:299-320.

Lemon, R. (1984) Methods for Neuronal Recording in Conscious Animals. IBRO Handbook Series: Methods in the Neurosciences, Vol. 4. John Wiley and Sons, Chichester.

Lynch, J.C., Mountcastle, V.B., Talbot, W.H., and Yin, T.C.T. (1977) Parietal lobe mechanisms for directed visual attention. J. Neurophysiol.40:362-389.

Mackay, W.A., and Crammond, D.J. (1987) Neuronal correlates in posterior parietal lobe of the expectation of events. (In prep.)

Mauritz, K.-H., and Wise, S.P. (1986) Premotor cortex of the rhesus monkey: Neuronal activity in anticipation of predictable environmental events. Exp. Brain Res. 61:229-244.

Mishkin, M. (1979) Analagous neural models for tactual and visual learning. Neuropsychologia 17:139-151.

Mishkin, M. (1982) A memory system in the monkey. Phil. Trans. Roy. Soc. Lond. [Biol.] 298:85-95.

Mistlin, A.J., Perrett, D.I., and Chitty, A.J. (1986) Somatosensory and associated visual properties of neurones in a polysensory region of macaque temporal cortex: A preliminary study. Behav. Brain Res. 20:120.

Mountcastle, V.B., Lynch, J.C., Georgopoulos, A., Sakata, H., and Acuna, C. (1975) Posterior parietal association cortex of the monkey: Command functions for operations within extrapersonal space. J. Neurophysiol. 38:871-908.

Murray, E.A., and Mishkin, M. (1984) Relative contributions of SII and area 5 to tactile discrimination in monkeys. Behav. Brain Res. 11:67-83.

Murray, E.A., Nakamura, R.K., and Mishkin, M. (1980) A possible cortical pathway for somatosensory processing in monkeys. Soc. Neurosci. Abstr. 6:654.

Niki, H., and Watanabe, M. (1979) Prefrontal and cingulate unit activity during timing behaviour in the monkey. Brain Res. 171:213-224.

Perrett, D.I., Smith, P.A.J., Mistlin, A.J., Chitty, A.J., Head, A.S., Potter, D.D., Broennimann, R., Milner, A.D., and Jeeves, M.A. (1985a) Visual analysis of body movements by neurones in the temporal cortex of the macaque monkey: A preliminary report. Behav. Brain Res. 16:153-170.

Perrett, D.I., Smith, P.A.J., Potter, D.D., Mistlin, A.J., Head, A.S., Milner, A.D., and Jeeves, M.A. (1984) Neurones responsive to faces in the temporal cortex: Studies of functional organization, sensitivity to identity and relation to perception. Human Neurobiol. 3:197-208.

Perrett, D.I., Smith, P.A.J., Potter, D.D., Mistlin, A.J., Head, A.S., Milner, .D., and Jeeves, M.A. (1985b) Visual cells in the temporal cortex sensitive to face view and gaze direction. Proc. Roy. Soc. Lond. B 223:293-317.

Seltzer, B., and Pandya, D.N. (1978) Afferent cortical connections and architectonics of the superior temporal sulcus and surrounding cortex in the rhesus monkey. Brain Res. 149:1-24.

Seltzer, B., and Pandya, D.N. (1984) Further observations on parieto-temporal connections in rhesus monkeys. Exp. Brain Res. 55:301-312.

CHAPTER 5

Behavioural investigations into the importance of facial and body attributes, and motion, on social communication in macaque monkeys.

5.1 Introduction

5.1.1 Face perception and facial configuration

The study of face perception in humans - especially in infants - has been extensive, increasing our knowledge of human social and perceptual development (e.g. Caron et al, 1973; Fantz, 1961, 1963; Goren et al, 1975; Haaf and Bell, 1967; Haaf, 1977; Hainline, 1978; Haith et al, 1977; Maurer and Salapatek, 1976). Responsiveness to faces is an important aspect of both human and infrahuman primate social behaviour yet equivalent behavioural investigations of face perception in infrahuman primates have not been so numerous (e.g. Humphrey, 1974; Keating and Keating, 1982; Kenney et al, 1979; Mendelson, 1982; Mendelson et al, 1982; Overman and Doty, 1982; Rosenfeld and van Hoesen, 1979; Sackett, 1965, 1966; Wu et al, 1980).

The human infant studies have dwelt upon many aspects of face perception and much debate has been channelled into whether face perception is innate or learned. Fantz (1961) first reported selective perception in infants for a facelike pattern. He observed that human infants (1-6 months) preferred to look at (i.e. fixated

more) a "real" schematic face rather than scrambled faces or control test patterns. Another study by Fantz (1963) reported that 10 hour - 5 day old infants significantly fixated a face pattern longer than either concentric circles, newspaper print or unpatterned coloured circular targets. Fantz's work could be cited as evidence for the innate perception of faces but Fantz himself stressed that the results implied only that a pattern with certain similarities to social objects has stimulus characteristics of intrinsic interest or stimulus value (Fantz, 1961).

The arguments against an innate ability for face perception were strengthened when studies failed to replicate Fantz's results (e.g. Koopman and Ames, 1968; Kagan et al, 1966). Goren et al's (1975) study demonstrating the ability of 9 minute old infants to discriminate between normal and scrambled face patterns still failed to convince some child psychologists of this discriminative ability in newborns. Discrimination between the normal arrangement of facial features and scrambled arrays is generally reported in infants only at 2 months (e.g. Maurer and Salapatek, 1976; Maurer and Barrera, 1981) or 4 months (Haaf, 1977) with visual preference paradigms or fixation times to stimuli. (With these older infants it is, of course, important to realize that face patterns may have learnt significance). However, the fact that neonatal infants have been shown <u>at all</u> to be able to distinguish face patterns (see also Bushnell, 1983; Ellis, personal communication) should suggest the validity of these findings.

One problem with the methodology employed to study the nature-nurture issue of face perception is that the responses used to measure this

capacity have varied between studies, from duration of eye fixations to degree of head turning to a stimulus. A negative result with any of these measures cannot be considered conclusive evidence that no discrimination between stimuli has been made (Salapatek, 1975) unless it can be demonstrated that the response measures employed were sensitive to the detection of any discrimination.

Meltzoff and Moore (1977) reported that human infants between 12 and 21 days of age could imitate specific gestures, modelled by adults, such as sequential finger movement, mouth opening and tongue protrusion. They suggested three potential underlying mechanisms for the neonates' responses: Shaping of the response by the model performing the gesture; an innate releasing mechanism where the sight of mouth opening triggers infants to open mouth in a reflexive manner; and the capacity to integrate visual and proprioceptive information.

The first mechanism proposed was dismissed through observing videotapes of the model's behaviours and the second thought unlikely given the organization and lack of stereotypy of the infants' differential responses to the gestures. So, Meltzoff and Moore (1977, 1983) concluded that imitation is mediated by a representational system that allows infants to unite within one common framework both visual and motor transformations of the face and body to create the match required.

Although a debate continues on what processes may be involved (Anisfeld, 1979; Masters, 1979; Jacobson and Kagan, 1979; Meltzoff and Moore, 1979) Field et al's (1982) findings that human neonates with an

average age of 36 hours could discriminate and imitate three facial expressions (happy, sad and surprised) posed by a live model, support Meltzoff and Moore's hypothesis. That human neonates can imitate adult facial gestures and expressions would seem therefore to support an innate view of face perception, and suggest that a sophisticated visual representation of the face is present at birth.

In monkeys the development of social responsivity to appropriate stimuli has been studied quite thoroughly (Foley, 1934; Kenney et al, 1979; Boothe et al, 1982; Mendelson, 1982) using visual fixation and scanning patterns as discriminators for face/non-face tasks and direction of eye gaze (Keating and Keating, 1982; Mendelson, 1982). But, no studies have been specifically designed to utilize the monkeys' social responses as discriminators between stimuli that naturally elicit such responses. That being said, monkeys have been observed to react to human faces and to mirrors with lipsmacking (an appeasement gesture) as early as 5 or 12 days (Mendelson, 1982; Kenney et al, 1979).

Sackett (1966) has shown that even monkeys without visual experience are sensitive to social stimuli, responding to pictures of threatening adult monkeys and infant monkeys. He observed that the threat and infant pictures produced a greater frequency of responses (at approximately 3 months of age) on measures of behaviour including vocalization, disturbance, play, exploration and activity (climbing) than pictures of playing, withdrawing, fearful or copulating monkeys, or controls with no monkeys in the pictures. Lever-touching to expose the subject to pictures was also markedly reduced for threat pictures

at about month 3. Sackett concluded that socially meaningful visual stimuli appear to have unlearned, prepotent, activating properties for socially naive infant monkeys.

It seems unlikely that monkeys could discriminate between facial gestures without possessing the capacity to perceive faces per se, unless these discriminations were achieved by exploiting one internal facial feature alone, such as the mouth or eyes. So, Sackett's data could be construed as evidence for innate face perception (the ability to detect facial configuration). But, it should be emphasized that during rearing Sackett's monkeys, although they never saw another monkey, were hand-reared by a human experimenter for 5-9 days. This visual experience may have been sufficient for the animals to acquire a recognition mechanism for faces. (It is not proposed,however, that monkeys' responses to complex social expressions could have been learned in this way.)

Tentative evidence that the monkeys can perceive facial configuration was presented by Keating and Keating (1982) in their study of the visual scan patterns of two rhesus monkeys viewing faces. The small sample (two monkeys) reduces the validity of a generalization as Keating and Keating themselves report individual differences in looking strategies. Nonetheless, they do report that, generally, less visual attention was paid to the rearranged schematic faces compared with the typical face. The rearranged faces included an upside-down face, an upright and a horizontal face with asymmetrically arranged features. The Keatings also reported that visual interest shifted away from the eyes for only some of the rearranged arrays

(predominantly the upright jumble). From these data it seems that at least part of the visual interest in faces is due to the facelike array of features.

Premack (1975) also investigated the perception of face configuration, in chimpanzees. He required that four chimpanzees (approximately 5-12 years of age) place face elements (two eyes, nose, mouth) in their veridical positions on a blanked out face of a chimpanzee, and observed that each animal's constructions differed significantly from the ideal face (position and/or identity of a facial element occupying that position). Premack's (1975) results can be interpreted in one of two ways: Either, chimpanzees cannot perceive face configuration; or chimpanzees can perceive face configuration but do not have the cognitive capacity to reconstruct adequately the disassembled figures.

This brief review of the monkey studies on face configuration reveals how limited the research into this area has been. In contrast to the human studies from which evidence is now emerging that tentatively supports an inborn system for the perception of face configuration, monkey studies into this aspect of face perception are limited in their findings. The largely inconclusive status of this work urges a definitive investigation into this question.

The first aim of this study was therefore to design an experimental methodology to investigate monkey's natural social responses to stimuli resembling faces and to those with rearranged or jumbled facial features to determine whether monkeys can perceive face configuration. Goren et al's (1975) study of human neonates'

responses to the natural and jumbled features of faces employed two-dimensional (2D) schematic stimuli. To ensure attentiveness stimuli used in this design had to be moved rather than held static. One criticism of the human infant face perception studies must be the use of unreal, often impoverished 2D stimuli that give a paucity of information. Salapatek (1975) and Spieker (1982) were just two who recognised the need for more ecologically valid stimuli in the form of dynamic (or animate), three-dimensional (3D) faces. Thus, it was decided to measure the monkeys' social responses to moving 3D models of monkey faces with the normal and jumbled arrangements of facial features. In contrast to the Keating's (1982) study, the rearranged faces included only upright faces but with both symmetrically and asymmetrically arranged internal features and a face with no internal features.

This experimental design was predisposed for application in two contexts: (1) the further investigation of whether the perception of face configuration is innate or acquired (through a social learning process) in primate infants reared in isolation; and (2) the isolation of perceptual and/or social disorders in monkeys with relevant cortical or subcortical lesions. Application towards the latter situation is described in Chapter 6.

5.1.2 Facial expression and posture

Studies of the behavioural repertoire of macaque monkeys have been executed by a number of authors (Bertrand, 1969; Chalmers, 1979;

Chevalier-Skolnikoff, 1974; Hinde and Rowell, 1962; van Hooff, 1962) who give detailed accounts of the social responses elicited by distinct gestures or postural displays. For each compound facial expression or gesture the elements comprising the display are defined. Yet, the efficacy of individual elements of the displays (or the combination of elements) has not been thoroughly specified. Obviously each element of the display must specify and characterize that display giving it a distinctive visual code. It would be of value to discern whether the independent expression elements bear equivalent behavioural importance or whether some cues supersede others in a natural context. van Hooff (1962) documented these expression elements and indicated that in the actual compound facial expressions a number of expression elements from different categories may be combined providing a large range of possibilities. Listed as expressions elements are: The eyes; the eyelids; the eyebrows and upper head skin; the ears; the mouth-corners; the lips; and the body posture (van Hooff, 1962).

Both Keating and Keating (1982) and Mendelson et al (1982) report the importance of the eye region of the face. Mendelson et al (1982) commented that 3 week old monkeys responded more emotionally (squirming, squealing and lipsmacking) to pictures of monkeys with eye contact rather than eye aversion. (Note also that the head was averted with the eyes.) Observing monkeys' scanning patterns Keating and Keating (1982) noted that for stimulus faces with dramatic mouth gestures eyes persisted in being the most fixated facial feature. Mouth gestures naturally play an important role in primate communication particularly in differentiating certain facial

expressions.

Most facial expressions are accompanied by a typical body posture. The gesture may contain forward head or body movements with the head lowered, or backward body movements; may constitute an erect static posture with the head raised; or the posture may be hunched or crouched (van Hooff, 1962). It is the function this role of body posture, more specifically head posture, serves in social communication that gives rise to the second study. The aim of this study was to assess monkeys' social responsiveness (as for the previous study) to postural cues accompanying facial displays.

Investigations of the role of head posture (or head view) in social gesturing were also stimulated by the neurophysiological studies in macaque monkeys reported later in this thesis (Chapter 7) and see Perrett et al (1984, 1985b). To summarize the relevant physiological findings: Populations of neurones in an area of the temporal lobe - the superior temporal sulcus (STS) - have been described which are selectively responsive to different head views. Five distinct 'prototypical' views with respect to the observing monkey appear to be coded by separate populations of neurones - full face, (left and right) profile, back of the head, face (or head) up and face (or head) down.

An investigation into the social importance of the two postures (head up and head down) on monkeys' behavioural responsivity was proposed for two reasons. First, from van Hooff's (1962) observations it is clear that the elevation of the head (raised or lowered relative to an

observing monkey) is often varied in social communication. Ethological studies indicate the employment of such visual cues by one monkey (the sender) in social interaction with a conspecific, but generally do not indicate that the same cues (by themselves) can be perceived and recognized by the conspecific (the receiver). Second, since neurophysiological studies reveal some cells selectively responsive to the head up/down views of the face, it seems likely that these head views can be discriminated at the behavioural level and that they possess an important role in social interactions.

Mendelson et al (1982) observed that pictures of faces with eye contact and with eye gaze averted in the horizontal plane evoked differential responses in the monkey. By presenting the test head postures (head up and down) with both eye contact to the observing subject and eyes averted vertically from the subject, the effect of direction of gaze manipulated in the vertical plane could be explored both independently and in combination with the head posture element. Social responsivity might be expected to be affected by either one or both of these cues.

5.1.3 Movement

Movement provides biologically important information about the nature and intent of animate objects over and above the static information about an object's form. Butler (1961) observed that motion pictures of primate social behaviour served to maintain rhesus monkeys' attention for longer periods of time than static photographs of

monkeys; which suggests perhaps that movement of an object alone may simply increase attentiveness towards that particular object.

Physiological investigations into movement sensitivity (Perrett et al, 1985a, 1987a) have revealed substantial populations of cells, in the STS, selectively responsive for different types of movement and stimulus form. For the majority of these movement-sensitive cells, different populations of neurones responded to particular movements of whole bodies or some part of them, e.g. the head or limbs. Perrett et al (1985a) have identified populations of cells sensitive to movements (either translations or rotations) along three orthogonal axes (towards and away from the monkey, left and right, and up and down). Considering just those cells sensitive to movement along the towards/away axis; one population of neurones were particularly responsive to translations of the face or body towards the monkey, a second to rotations that brought a face or body to confront the monkey. Further populations were selective for rotations turning the face or body away from the monkey, and for face/body translations away from the monkey.

One explanation proffered for such cells with conjoint sensitivity to form and motion, at the neural level, is that particular types of movement may be significant components in characterizing social expressions (Perrett et al, 1985a). For example, a forward head and body lunge is often an integral component in a primate threat gesture (Hinde and Rowell, 1962; van Hooff, 1962). This raises the question of whether form and motion act as a Gestalt to release particular social responses at the behavioural level?

So, a third study was designed to explore this contention by presenting a full-scale 3D model monkey (and socially irrelevant control stimuli) translating and rotating towards and away from the observing monkeys. Both types of movement were examined as the exact nature of the behavioural significance of neurones selective for 'rotate towards' and 'translate towards' movements is not obvious. The results may indicate that either type of movement (and underlying cell populations) is important in evoking the same behavioural response, or that the two types of movement effect disparate behavioural responses.

If both form and motion do play an integral role in characterizing social expressions, the monkeys would be expected to respond preferentially to particular movements of the face and/or body in one of the opposing directions; and remain unresponsive to equivalent movements of the non-face/body control objects.

5.2 General Methods

It is intended that this chapter provides a general description of the techniques used to investigate monkeys' natural capacity to discriminate certain facial and body attributes. The common methodological approach is described for three experiments investigating the differential responsiveness of monkeys to: (I) the proper arrangement of facial features and scrambled faces (i.e. face configuration); (II) head postures and direction of eye gaze; and

(III) the combined movements of the head and body. The specific experimental design and variations in stimuli and testing procedure are subsequently described for each experiment.

5.2.1 Subjects

The subjects providing data for analysis were selected from a captive social breeding colony of stumptail macaques (Macaca arctoides). They were not caged separately but housed with other members of the colony. The subjects ranged between 4 months and 10 years of age.

Five stumptail macaques, four females and one male, were selected for Experiment I. A larger subject group of nine macaques was available for Experiment II. This group included the five monkeys from Experiment I and four additional monkeys, two females and two males. For Experiment III it was necessary to drop one female and one male monkey from the previous experimental group as they became difficult to handle and unwilling to attend to the stimuli presented. One female stumptail (without previous experience of the stimuli) replaced one of these subjects.

5.2.2 Stimuli

(a) Experiment I: Face configuration

The test stimuli comprised five hand-made three-dimensional model monkey heads varying with respect to the position of the facial

features. The models were built with a papier mache base moulded to form the general face structure. Material fur was then attached to the base with contact adhesive defining the face-fur outline. Rubber latex was secured to the face area to replicate skin texture and coloured with indelible pens to simulate the facial pigment. A mouth was drawn onto the face with black pen and a nose shaped from latex and secured to the face with adhesive. A pair of glass eyes completed the facial features. The stimuli are illustrated in Figure 5.1.

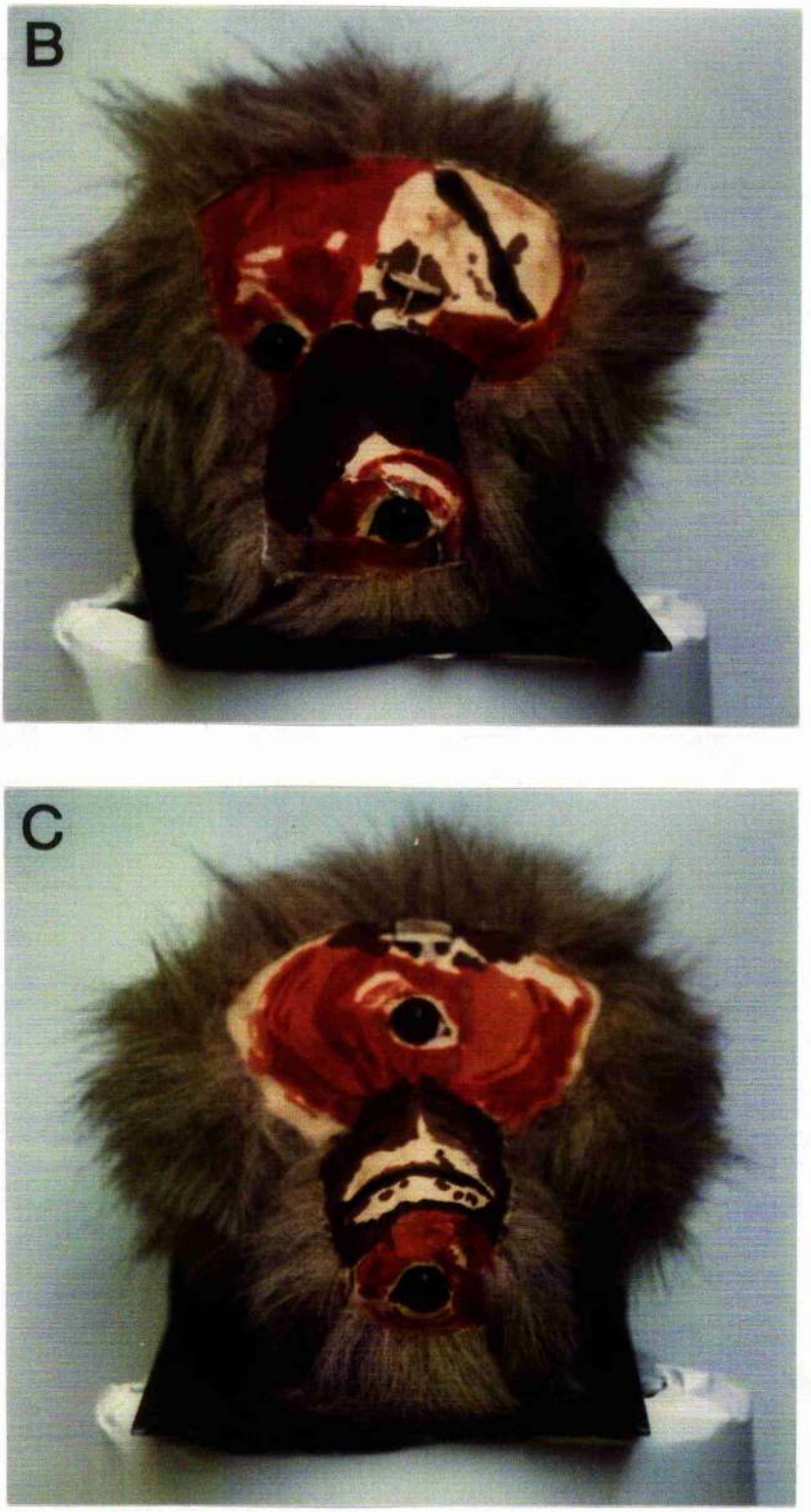
The 'normal' head model, N (Figure 5.1A) with the proper arrangement of facial features was modelled on an adult female stumptail macaque who possessed distinctive red pigment (characteristic of these animals) around the eye region of the face. The facial features were scrambled or jumbled for three head models (J1, J2, J3, see Figure 5.1B-D) both asymmetrically (J1) and symmetrically (J2 and J3). In scrambling the facial features an effort was made to assign the appropriate facial pigment to each feature. A fifth model was entirely devoid of internal facial features, i.e. blank (B, Figure 5.1E) although the facial outline delineated by fur was maintained.

Each model was mounted on an aluminium steel holder, 20cm by 15cm by 10cm (height), enabling each head model to be presented (at eye level or below to the subject) with all the facial features visible. These steel holders were inconspicuous and eliminated any variability in orientation of the stimuli and increased ease of presentation.

(b) Experiment II: Head posture

A life-size model of the dominant male stumptail macaque in the social

Figure 5.1 Stimulus set of modelled monkey heads with variation in configuration of the facial features. A, model N - normally arranged facial features; B, model J1 - asymmetrically jumbled features; C, model J2 - jumbled features with eyes vertically symmetrical; D, model J3 - as (C) but with eyes horizontally symmetrical; E, model B - face/fur outline with no internal facial features.



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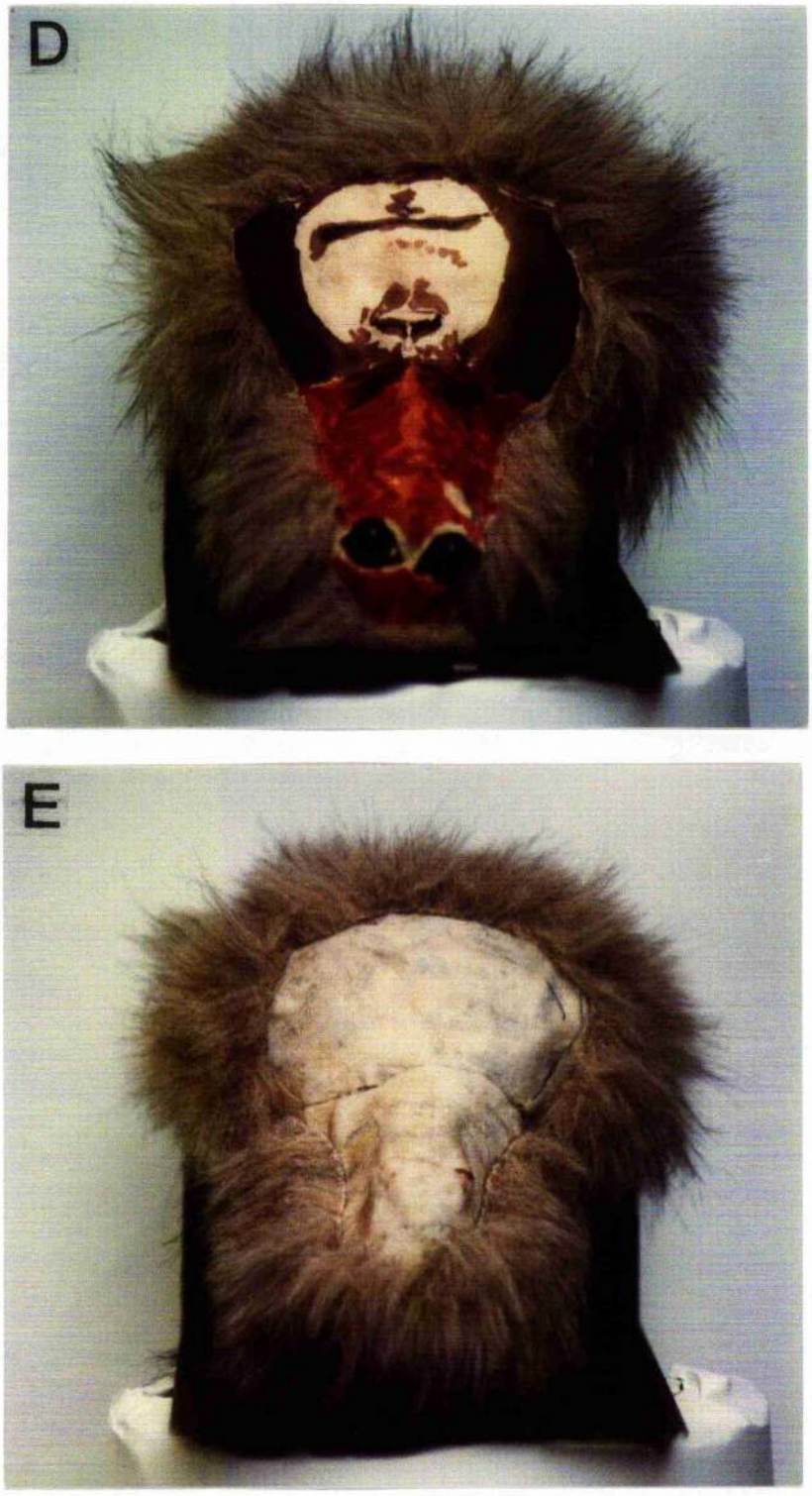

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colony was commissioned from a theatre designer for Experiments II and III. The components of the model - the head, the torso and the limbs - were initially modelled in clay from photographs and actual measurements of the subject monkey. A negative cast in plaster of paris was constructed and finally a positive cast made of papier mache. Surface texture was created using a mixture of latex and emulsion paint and the surface details were subsequently painted on.

The components were assembled with an internal wooden frame with universal camera stand joints at the points of articulation, allowing mobility of the head and limbs. The completed model was then covered appropriately with artificial fur. To complete the authenticity of the model, clear glass eyes (with the appropriate pigment marked with indelible pens) were inserted in eye sockets in the face in such a way as to allow horizontal and vertical movement of the eyeball.

The model was arranged in a crouched position and the test stimuli defined through different combinations of head and eye angle respectively. The stimuli are illustrated in Figure 5.2, photographed from the same viewing position as the expected subjects. The stimuli were termed:

(a) HoEo (Head normal, Eye contact), where the head (axis from ear through snout) is normal to the axis of the torso - the snout pointing at the observer (0 degrees) - and the line of eye gaze is parallel to this axis, i.e. in eye contact with the observer (Figure 5.2A);

(b) HdEo (Head down, Eye contact), where the head faces down (or the axis through the snout lies) at an angle approximately 45 degrees to the axis of the torso, but the direction of eye gaze remains normal to

this axis, at 0 degrees to the observer (Figure 5.2B);

(c) HdEd (Head down, Eyes down), where the head is as in (b) but the direction of eye gaze is parallel to the axis through the snout, i.e. the eyes are aligned with the head facing down with respect to an observer (Figure 5.2C);

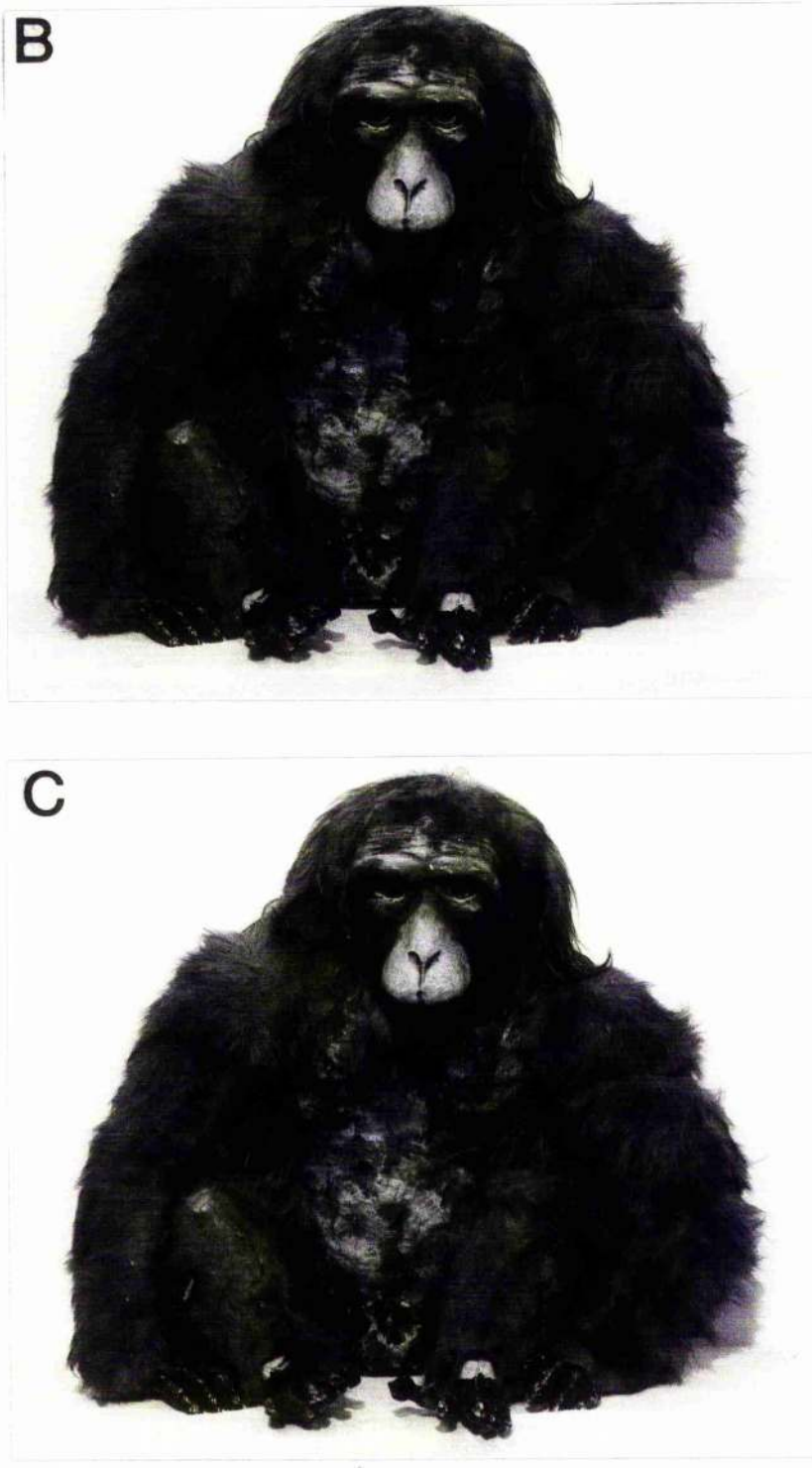
(d) HuEo (Head up, Eye contact), where the head faces up (or the axis through the snout lies) at an angle approximately 45 degrees to the axis of the torso, but the direction of eye gaze remains normal to this axis, at 0 degrees to the observer (Figure 5.2D); and

(e) HuEu (Head up, Eyes up), where the head angle is as in (d) but the direction of gaze is parallel to the axis running through the snout, i.e. the eyes are aligned with the head facing up with respect to the observer (Figure 5.2E).

(c) Experiment III: Movement

The full-scale model monkey positioned as in (a) of Experiment II was used as the stimulus for this experiment. (No changes in the monkey's posture were necessary.) In this study dynamic features as opposed to the static physical properties of the stimulus were varied with each experimental condition. Whole body movements of the model monkey constituted the test stimuli, namely: (a) a movement towards the monkey, or loom; (b) a movement away from the monkey, or retreat; (c) a rotation of the model monkey's body and head simultaneously towards the subject from a profile view (face turned 90 degrees away from the observer) to the full-frontal face view; and (d) a rotation of the stimulus as above away from the subject from the full-frontal face to profile view.

Figure 5.2 Life-sized stimulus model of a macaque monkey with various combinations of head and eye angle. A, HoEo; B, HdEo; C, HdEd; D, HuEo; E, HuEu. H, head angle; E; eye angle; o, eye-level with viewer; u, up 45 degrees from o; d, down 45 degrees from o.



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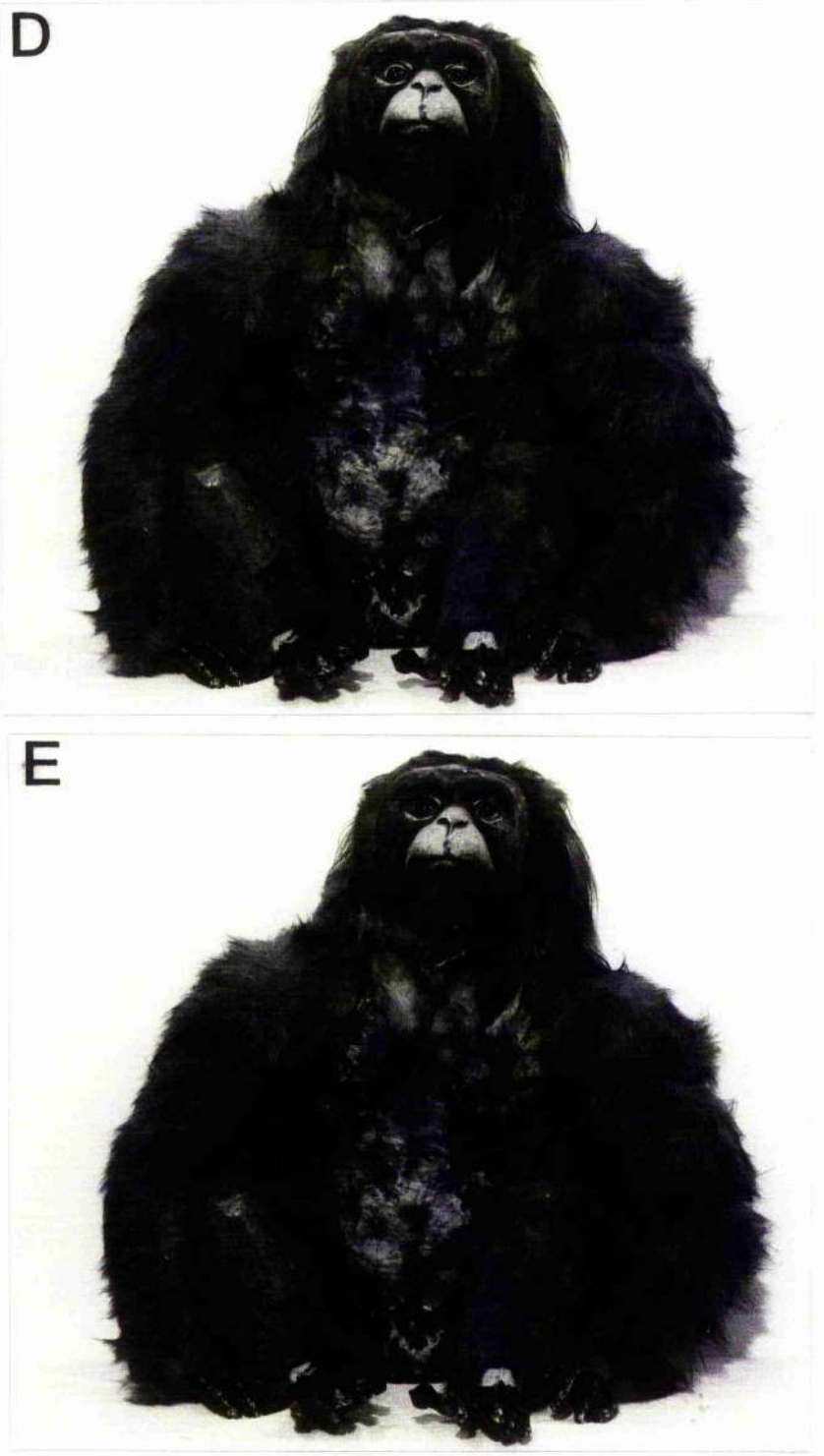

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Three-dimensional inanimate non-face stimuli presented in the same manner as the test stimuli acted as controls in each of the three experiments. These stimuli were selected from objects in and around the laboratory, and included patterned material of different colours and textures, arousing objects such as fur and food, and other objects of a variety of shapes and sizes, e.g. plastic bag, dustpan, ball. (In Experiments II and III the control objects were placed on the model, previously covered with a sheet of black material.)

5.2.3 Apparatus

All behavioural testing took place in an adapted Wisconsin General Test Apparatus (WGTA) whose basic structure is shown in Figure 5.3. Two hollow compartments are separated by an opaque partition which may be raised or lowered by a pulley system operated by the experimenter. The rear compartment houses the subject (in a travelling cage with a transparent perspex front) and stimuli are traditionally placed within the front compartment for presentation to the monkey.

The front screen was covered on its inner face with a sheet of black card 64cm square to prevent the subject inadvertently viewing its own reflection. Where necessary, a small piece of card (8cm square) from the upper corner of the front screen could be removed to allow filming of the subject during the testing sessions.

A section of the wooden roof of the front compartment of the WGTA was removed and a sheet of perspex (32cm square) inserted in its place.

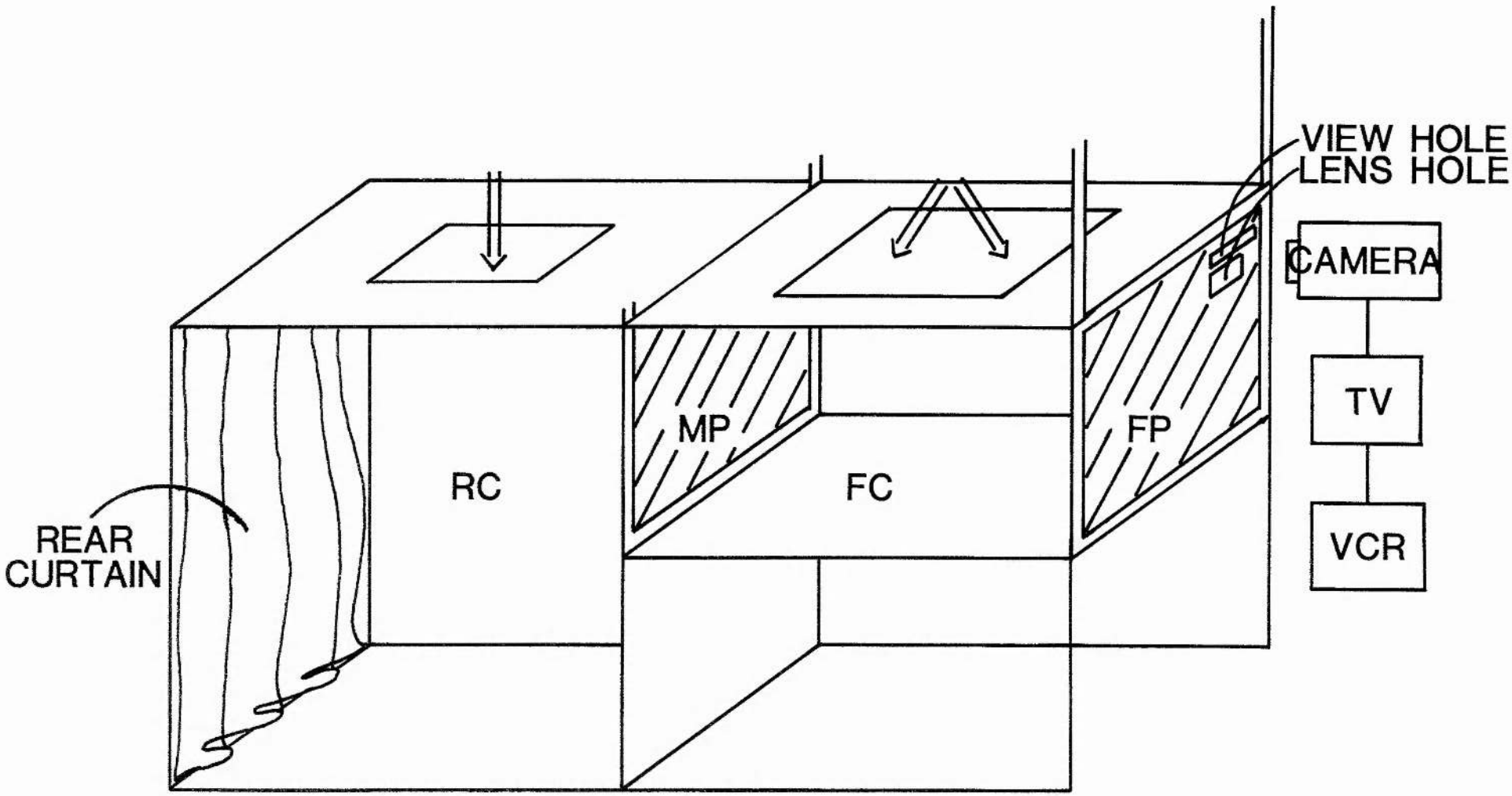


Figure 5.3 Wisconsin General Test Aparatus (WGTA) for primate behavioural testing. The rear compartment (RC), housing the subject monkey, is separated from the front compartment (FC), in which stimuli are presented, by the middle partition (MP). Both this partition and the front one (FP) can be raised and lowered to accommodate presentation and viewing of the stimuli. The monkey's behavioural responses are observed by a camera through the FP and recorded and displayed by a video cassette recorder (VCR) and television monitor (TV).

Illumination from 60W lamps was then directed forward onto the stimulus and backward onto the subject through this section. Additional external sources of light were used to increase illumination of the stimuli in Experiments II and III where a stimulus was presented to the subjects from outside the WGTA.

The subjects' behavioural responses over the test period were continuously filmed by a Canon VC-20 colour video camera and the data recorded on a Panasonic VHS portable video cassette recorder for analysis. A video monitor (Sony VFA 0014) connected directly to the video camera aided monitoring of the subjects' attention to stimuli.

(a) Experiment I

Two parallel rails were placed centrally (25cm apart) on the presentation shelf in the front compartment. A stimulus presentation platform on wheels could be moved between these rails, directly towards and away from the subject (a standard distance).

(b) Experiment II

The apparatus used for this experiment is described in detail below, for Experiment III. The stimulus model monkey was simply secured with binding to the platform seat of this apparatus in a static position.

(c) Experiment III

A system was designed specifically for the WGTA in order that the stimulus model monkey could be made to translate or rotate towards or away from the subjects (in the WGTA) consistently and easily. The apparatus was constructed of three essential elements: (1) a trolley

frame (Figure 5.4A); (2) a trolley and (3) a platform seat (Figure 5.4B). The trolley frame's free-standing wooden structure (200cm by 60cm) was built to fit into the base of the front compartment of the WGTA. Strips of aluminium Grippa-shelf support were fixed to the long sides of the trolley frame along which the wheels of the trolley (a wooden structure 60cm by 40cm) could run. A pulley system was attached to the main frame by which the trolley bearing the platform seat could be systematically manoeuvered. The platform seat, adjustable in height by rotation, was fitted to the trolley through the central cross-strut of the trolley (see Figure 5.4B). A stimulus placed on the platform seat could therefore be made to translate and rotate towards or away from the subject. Stoppers were placed on the track 50cm apart so that the distance travelled forward and back was constant.

5.2.4 General procedure

The subject was transferred from the colony into a travelling cage, transported to the testing room, and placed in the rear compartment of the WGTA. A material backdrop at the rear of the WGTA was secured to reduce distractions during the testing period. When the monkey was in a quiet, alert state, the recording apparatus was activated and the stimuli presented. In between blocks of ten trials, where one block consists of each of the test stimuli plus an equivalent number of controls, the subject was given a food reward for two minutes. Each of four blocks was recorded on film and each stimulus verbally identified in order of presentation. At the testing session's

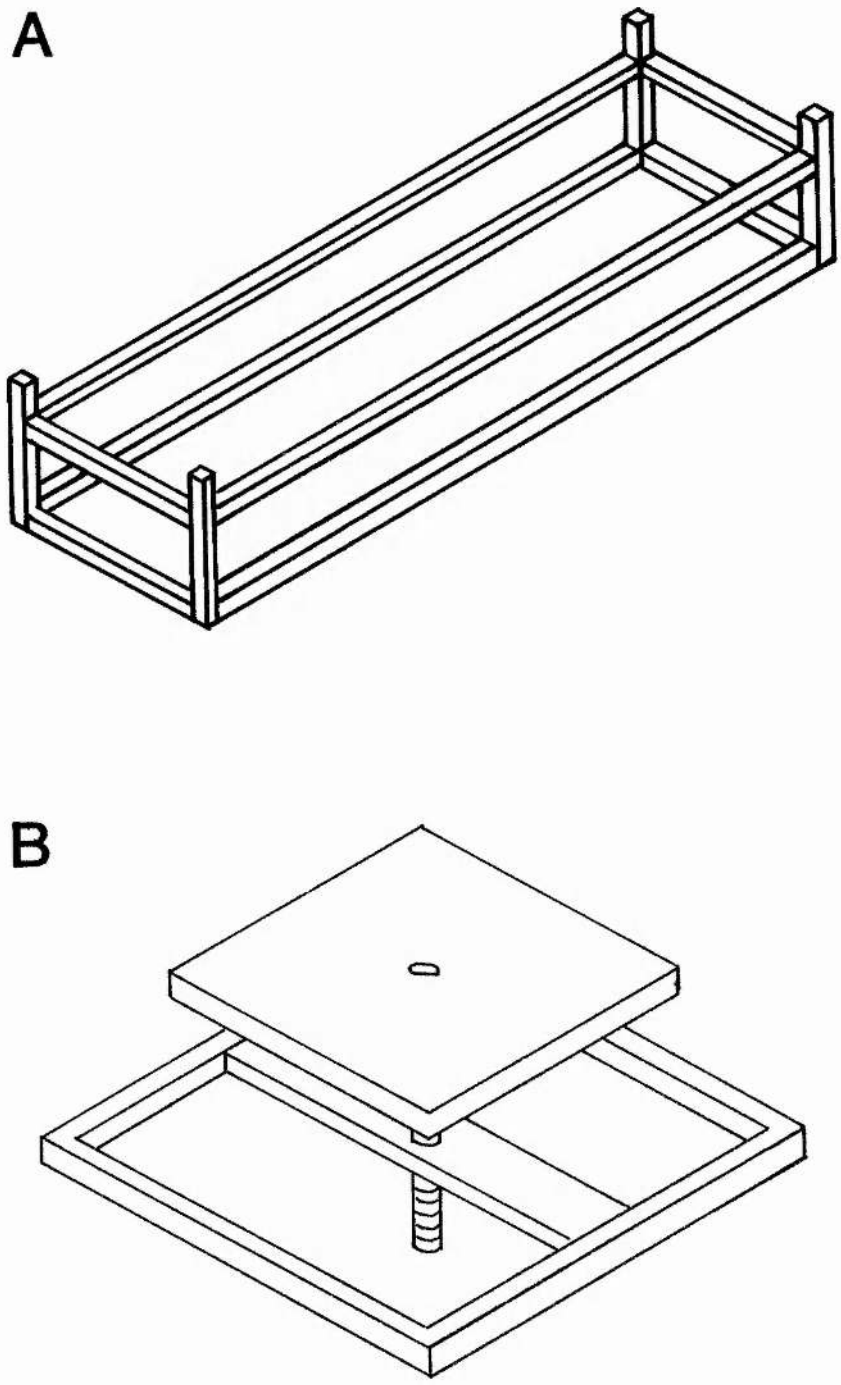


Figure 5.4 Apparatus for translation and rotation of stimuli for presentation in the WGTA. A, secure trolley frame with end stops; B, translating trolley with rotating, height-adjustable, platform seat for stimuli. (Not drawn to scale.)

conclusion, the subject received a final food reward and was returned to the colony.

5.2.5 Stimulus presentation

The stimuli were presented in blocks, each consisting of the test stimuli and an equivalent number of controls (five test stimuli and five controls for Experiments I and II, and four test stimuli and four controls for Experiment III). The total presentation time for each stimulus (trial) was four seconds, with an intertrial interval between 30 seconds and 1 minute. Between blocks (presented on the same day) a 5 minute interval was observed. The order of presentation of the stimuli within and between blocks was randomized except that the first stimulus was always a control object. The subjects were given four blocks of trials for each experiment. These blocks were split evenly over two days, i.e. two blocks per day for each experiment, and the separate experiments were performed 4-5 months apart. The subjects were tested on each experiment in sequence, i.e. first on Experiment I, then Experiment II and finally Experiment III.

(a) Experiment I

In one trial a test stimulus or a control object was placed on the stimulus presentation platform, 40cm from the subject, in the front compartment with the partition lowered. The front screen was then lowered, the partition raised, and the platform bearing the stimulus guided slowly forward 30cm in 1 second, held in this position for 2 seconds, and then moved back to its original position in 1 second.

The trial was terminated after the 4 second stimulus presentation by lowering the partition. The stimulus was then changed and the procedure repeated for the remaining trials.

(b) Experiment II

The model monkey was secured to the platform seat approximately 70cm from the subject and its head and eye angle adjusted for each presentation. Prior to the experimental testing sessions the average position of a subject's head in the travelling cage in the WGTA was ascertained and the stimulus set up so that its head would be on a level with the subject's. A marker was then calibrated to determine the angle at which the head and eyes should lie for each stimulus condition. With the stimulus in position the front screen was raised (the partition remained raised throughout this experiment) and the stimulus presented for 4 seconds. The trial was terminated by lowering the front screen. With a new stimulus this procedure was repeated for the remaining trials.

(c) Experiment III

Initially the model monkey stimulus was fixed in a HoEo pose, as in (b). For a looming movement the stimulus was positioned 120cm from the subject, the front screen raised (again the partition was constantly raised) and the stimulus moved forward 50cm over 4 seconds total presentation time (approximately 12cm/s) by a pulley system operated by the experimenter. The trial was terminated by lowering the front screen. For a retreating movement the stimulus was positioned 70cm from the subject and moved back 50cm over 4 seconds. Rotations through 90 degrees from full-frontal face (HoEo) to a

profile view of the monkey - rotate away, RA - or from profile to full-frontal face - rotate towards, RT - were hand manipulated at a velocity of approximately 20 degrees/s. Rotations were in progress throughout the 4 second presentation period. Control objects in place of the test stimuli were manouvered in the same manner.

5.2.6 Response measure and data collection

The frequency with which specific appeasement gestures were observed in response to the stimuli presented was measured. These gestures included both teeth-chattering and lipsmacking - appeasement responses elicited by the same stimuli. These facial gestures were treated equally as they merely represent different levels of intensity of appeasement. Other mouth movements such as chewing and occasional vocalizations, identified separately from the opening and closing cycles of the mouth observed in appeasement gesturing, were not included for data analysis.

5.3 Results

The data from the three experiments, subject to the same analytical treatment, are described separately for each experiment.

5.3.1 Experiment I: Face configuration

The effect of conditions and blocks of trials on responsiveness of the subjects was investigated. The number of appeasement gestures, for each subject, elicited by each stimulus in a block of trials were analysed by a 5 (subject) X 4 (test block) X 6 (condition) analysis of variance (ANOVA). The analysis revealed a main condition effect, $F(5,20)=11.98$, $p<0.0001$. These data (appeasement response and the standard error mean (S.E.M.) for each stimulus condition) are presented in Table 4A.

Post hoc analysis revealed that the normal model, the monkey head with the proper arrangement of facial features, elicited a significantly larger appeasement response ($p<0.05$ Newman Keuls, each comparison) than any of the jumbled models, the blank or control objects (illustrated in Figure 5.5). These latter stimulus conditions did not differ significantly from each other although one model, J1, did elicit a greater response than the controls, which approached significance at $p=0.077$.

Figure 5.5 indicates a directional decline in responsiveness from N to J1, through J2, J3 and B, to C, which although simply a trend in the data could be suggestive of some kind of rank ordering of the jumbled head models with respect to 'faceness', i.e. how like the normal model they are. The jumbles were ordered numerically from J1 to J3 by this experimenter (subjectively) on their similarity to the normal model (but see Appendix C), and the decrease in responsiveness to the models mirrored this ordering.

The presence of internal facial features did not affect the subjects'

Table 4A Effect of face configuration on appeasement responses

	STIMULUS CONDITION					
	N	J1	J2	J3	B	C
MEAN APPEASEMENT RESPONSE	3.8	1.6	1.0	0.7	0.2	0.03
S.E.M.	0.9	0.5	0.4	0.3	0.15	0.02

Table 4B Habituation effect on appeasement responses with repeated stimulus testing

	TEST BLOCK			
	1	2	3	4
MEAN APPEASEMENT RESPONSE	2.7	1.6	0.5	0.2
S.E.M.	0.6	0.5	0.3	0.1

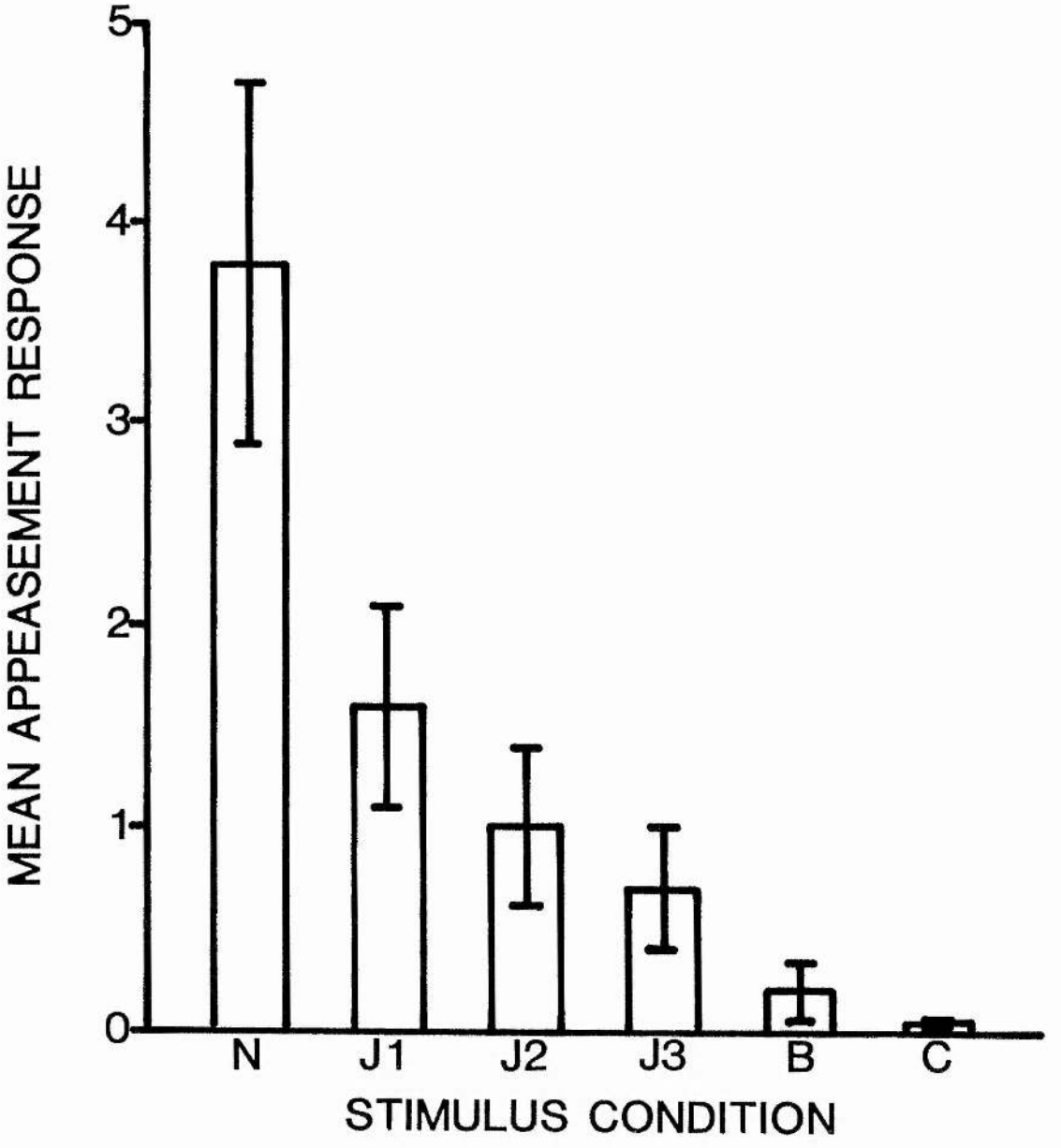


Figure 5.5 Sensitivity to face configuration. The mean and standard error response (five subjects) is given for each stimulus condition. A large appeasement response was given to the model monkey head with normal features (N), but not to any of the models with jumbled features (J1-J3), the blank model (B), or the non-face (control) objects.

responsiveness as no significant differences between the jumbled models (with internal features) and the blank (with no internal features) was noted. If symmetry in the arrangement of facial features was important for discriminating the normal model from jumbled models this was not obvious, as no significant increase in responsiveness to the symmetrical jumbles (either J2 or J3) over the asymmetrical jumble (J1) was observed. Indeed, if any discrimination between the jumbles was made, it would appear from above that it was more likely in favour of the jumble, J1.

The lack of response to the control objects, but more specifically the discrimination between the test stimulus conditions, dismisses any suggestions that the looming movements of the stimulus alone could account for the responses witnessed.

Although potentially more salient than line drawings or two-dimensional pictures of monkey faces, habituation to the three-dimensional model monkey heads was observed. There was a block effect, $F(3,12)=12.42$, $p<0.0005$, and a Condition X Block interaction, $F(15,60)=4.09$, $p<0.0001$. The overall responsiveness of the subjects for each test block of trials, calculated as the mean appeasement response for all conditions in the test block, are presented in Table 4B. The subjects' responsiveness to all the stimuli decreased significantly from block 1 to block 2 ($p<0.05$ Newman Keuls), block 1 to block 3 ($p<0.01$), block 1 to block 4 ($p<0.01$), block 2 to block 3 ($p<0.05$) and from block 2 to block 4 ($p<0.05$), as illustrated in Figure 5.6. Thus habituation to the three-dimensional model monkey heads was prominent in Experiment I where a decline in responsiveness

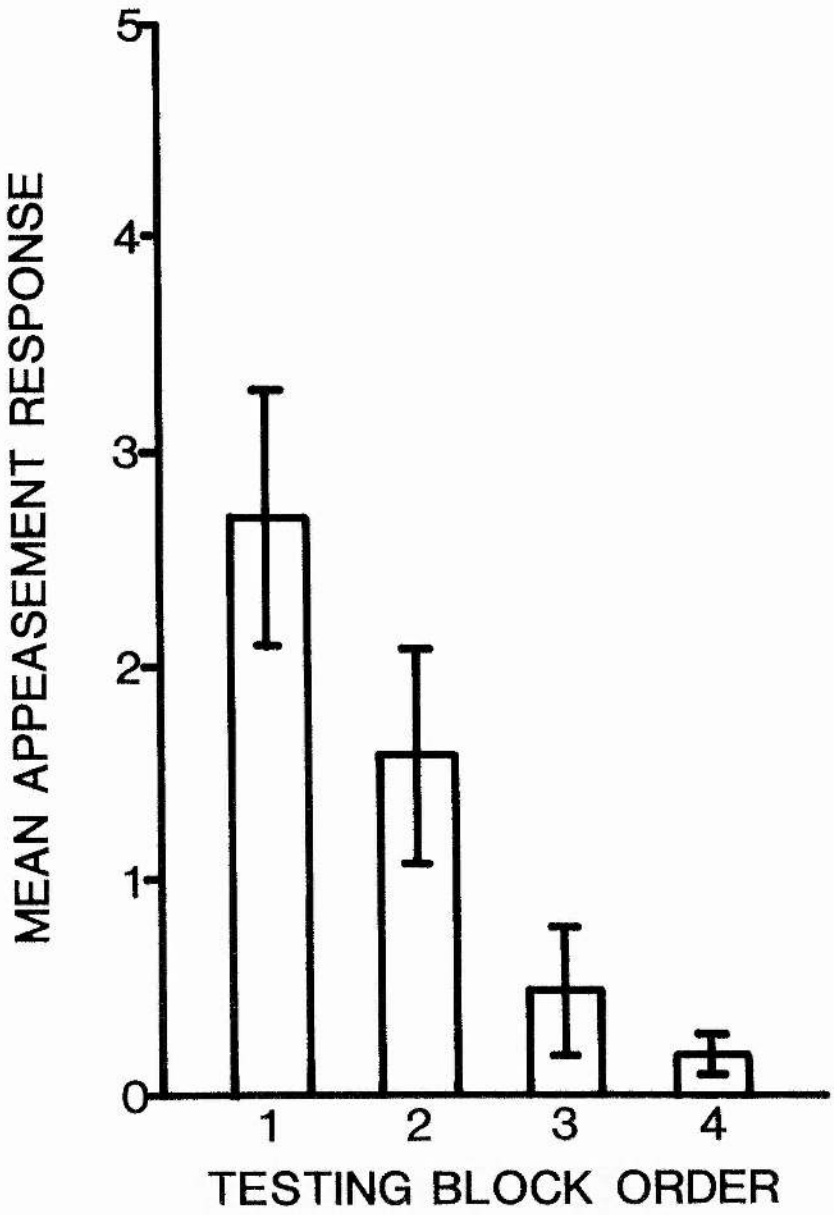


Figure 5.6 Habituation of appeasement response to face configuration stimuli. Mean and standard error responses to progressive testing (in blocks) of the configuration stimuli show a decline in overall responsiveness to the head model stimuli.

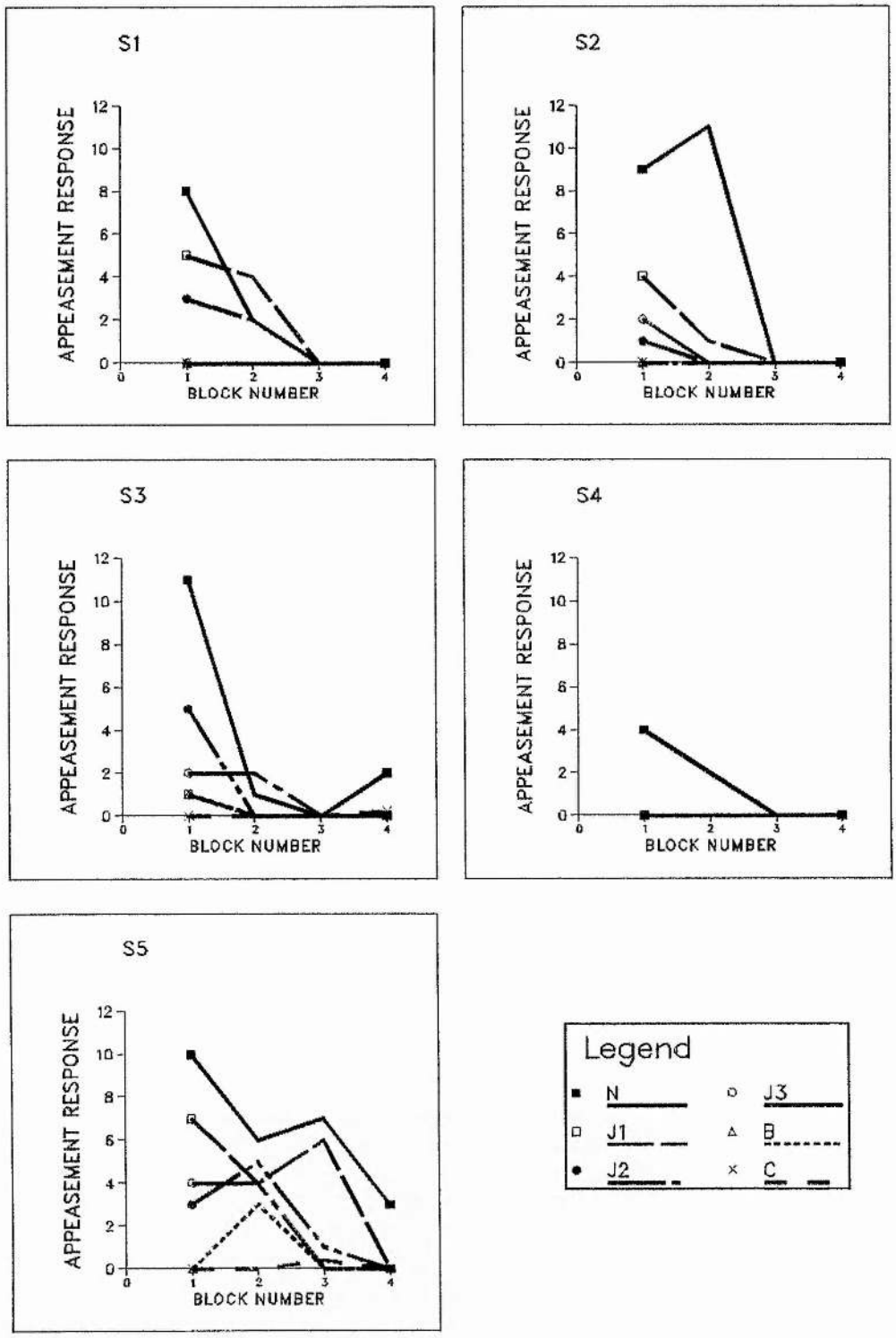


Figure 5.7 Individual sensitivity of five subjects to the normal configuration of facial features. Appeasement responses for subject monkeys S1-S5 are given for each of the stimulus conditions (indicated in the legend) over four blocks of trials.

to the test stimuli was observed over 4 blocks of trials. As the subjects' responses to control objects from the beginning of the testing period were almost negligible no habituation of this response could be dectected. A response to no more than 2 of 100 control trials presented was noted for each subject.

The individual responses of each subject are illustrated in Figure 5.7. They show the combined effects of a greater sensitivity to the normal facial configuration, a reduced sensitivity for jumbled facial features, an almost negligible response to control stimuli, and the decline in overall responsiveness from the first test block of trials to the final block of trials. It is interesting to observe that one subject, S4, is totally unresponsive to all stimuli except the normal model, N. This indicates, perhaps, how powerful the normal configuration of facial features is on the behaviour of a monkey.

5.3.2 Experiment II: Head posture

The effect of conditions and blocks on responsiveness of the subjects was investigated as in Experiment I by considering the number of appeasement gestures, for each subject, elicited by each stimulus in a block of trials. The mean appeasement response (and the standard error) for each stimulus condition are indicated in Table 5A and illustrated in Figure 5.8. These data were analysed by a 9 (subject) X 4 (block) X 6 (condition) ANOVA which revealed a condition effect, $F(5,40)=10.10$, $p<0.0001$. The normal head posture (HoEo), i.e. eye contact and head level with the subject (observer) produces a significantly greater appeasement response ($p<0.01$ Newman Keuls each

Table 5A Effect of head posture on appeasement responses

	STIMULUS CONDITION					
	HoEo	HdEo	HdEd	HuEo	HuEu	C
MEAN APPEASEMENT RESPONSE	6.4	4.6	4.6	0.6	0.5	0.03
S.E.M.	0.9	0.9	0.9	0.2	0.2	0.03

Table 5B No habituation effect on appeasement responses with repeated stimulus testing

	TEST BLOCK			
	1	2	3	4
MEAN APPEASEMENT RESPONSE	3.3	2.4	2.2	3.1
S.E.M.	0.7	0.6	0.5	0.7

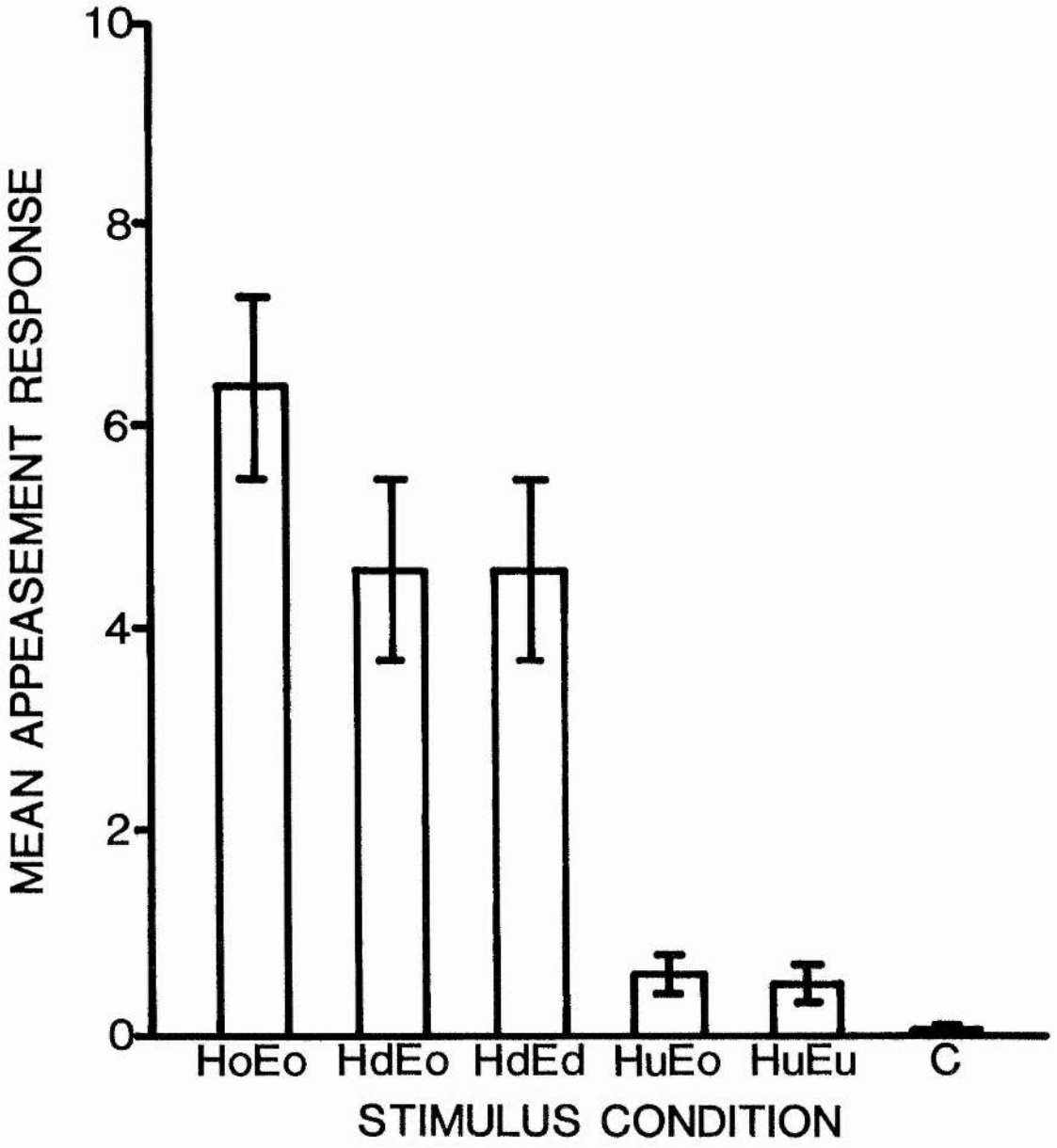


Figure 5.8 Sensitivity to head posture. The mean and standard error (nine subjects) appeasement response is given for each stimulus condition. Large responses are seen to the full face (Ho) and head down (Hd) postures, with reduced responses to the head up (Hu) postures and non-face (control) objects. Sensitivity to the direction of eye gaze is not evident here.

comparison) than either of the head up postures (HuEo - head up/eye contact, or HuEu - head up/eyes up) or the control objects. No significant difference in the level of responsiveness between the HoEo posture and the head down postures (either HdEo - head down/eye contact, or HdEd - head down/eyes down) was observed. Comparable with the HoEo posture the head down postures produced significantly greater appeasement responses ($p<0.01$ each comparison) than either of the head up postures or the control objects. Subjects' responses to the head up postures and control objects did not differ significantly.

The HoEo posture and head down postures of the model were equally salient as threatening stimuli resulting in the same intensity of submissive responses from the subjects whereas the head up postures induced no such submissive responses.

No significant difference was detected between the HoEo posture and the head down postures overall, but studying the individual responsiveness of the subjects to each stimulus condition (in Figure 5.9) there is a suggestion that the HoEo head pose may elicit a greater response than either of the head down postures. The summed response over 4 trials to the HoEo pose for five out of the nine subjects was greater than to either of the head down poses. One subject, S3, did not respond to the stimuli at all except for a small response to one stimulus (HuEo) which coincided with its presentation as the first test trial in the first block. This response could therefore be accounted for as a novelty effect.

Considering the direction of eye gaze of the model stimuli no obvious

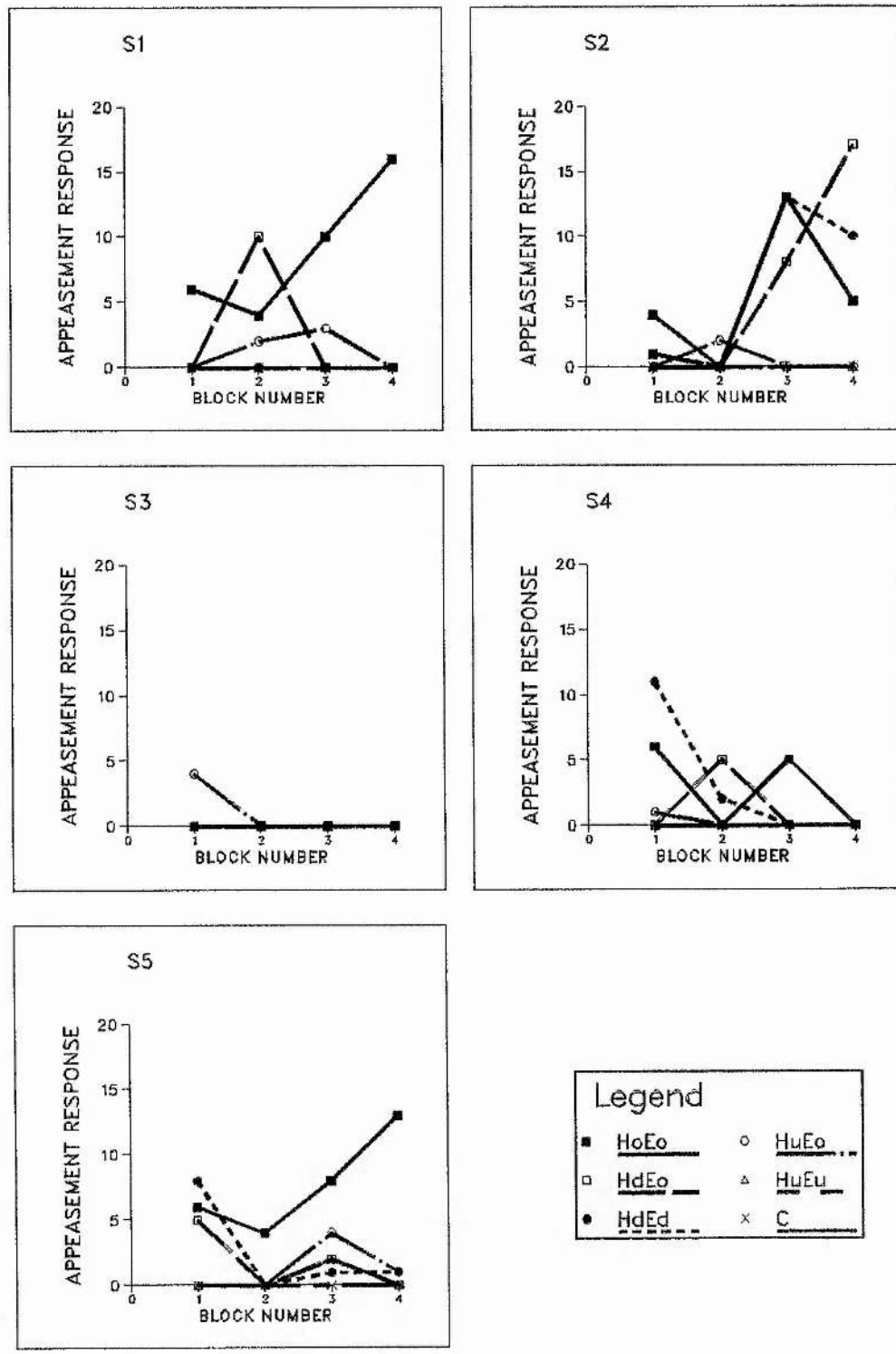
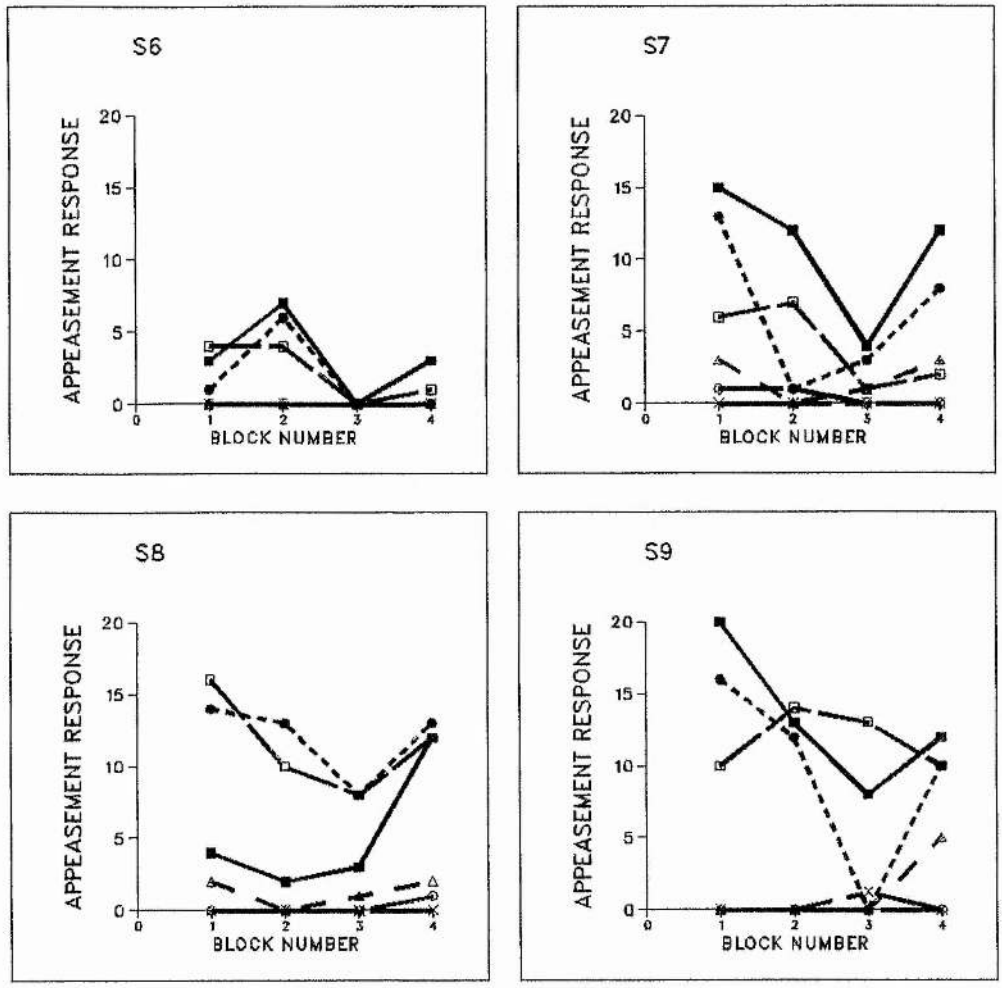


Figure 5.9 Individual sensitivity of nine subjects to head posture. Appeasement responses for subject monkeys S1-S9 are given for each of the stimulus conditions (indicated in the legend) over four blocks of trials.


S6
S7
S8
S9
APPEASEMENT RESPONSE
BLOCK NUMBER
0
5
10
15
20
1
2
3
4
Legend
HoEo
HuEo
HdEo
HuEu
HdEd
C

effect of eye contact versus eye aversion was observed. No significant difference in responsiveness within the head down postures or the head up postures between HdEo (eye contact) and HdEd (eye aversion), or HuEo (eye contact) and HuEu (eye aversion) was seen (Figure 5.8). One caveat however: The lighting conditions in the experimental set-up may not have adequately illuminated the eyes of the model monkey, as a heavy brow ridge sitting above the eyes may have cast shadow over them. It is more likely that when the two behavioural indicators of head posture and eye gaze are compounded, head posture is the more salient cue. This will be discussed in more detail in section 5.4.2.

Unlike the habituation of response to the head models seen in Experiment I, no such effect was seen to the full-scale model monkey in Experiment II. Analysis of variance of the overall responsiveness of the subjects to stimulus conditions over the four test blocks did not differ significantly (cf. Table 5B). Further investigation of the monkeys' behavioural responses using this three-dimensional model monkey as a stimulus was, therefore, possible with subjects with prior knowledge of the stimulus.

5.3.3 Experiment III: Movement

To recap, the types of face and body motion investigated in this experiment were divided into two categories: (a) translations toward or away from the (subject) monkey; and (b) rotations toward and away from the monkey. Comparisons with the opposing direction of motion

for both the model monkey and the control objects were thus made within one category of motion, i.e. either translations or rotations. The mean and standard error of appeasement response indicating the level of responsiveness of the subjects to each stimulus condition is indicated in Table 6A and 6B, and illustrated in Figure 5.10. These data were analysed by an 8 (subject) X 4 (block) X 6 (condition) ANOVA which revealed a condition effect, $F(7,49)=13.84$, $p<0.0000$, and a Condition X Block interaction, $F(21,147)=2.33$, $p<0.0013$. Post hoc analysis (Newman Keuls) of the data from each category of motion are considered separately.

(a) Translations

The model monkey (in HoEo pose) translating towards the subject elicited a significantly greater response ($p<0.01$) than the same stimulus moving away from the subject. The model translating towards the subject also elicited a greater response (significant at $p<0.01$ each comparison) than a control object moving either towards or away from the subject. There was no significant difference between the model translating away from the subject and a control either translating away or towards the subject. The control objects elicited no behavioural response from from the subjects at all. This is shown in Figure 5.10A.

Both form and motion of the stimulus were important in determining a subject's response as the subjects made a combined discrimination within and between dynamic aspects of this task. Discriminations were observed between: (i) the model and control stimuli moving equivalently in the optimum direction of motion; and (ii) the model

Table 6A Effect of translation movements and form of the stimulus on appeasement responses

	STIMULUS CONDITION			
	MODEL MONKEY		CONTROL	
	TOWARD	AWAY	TOWARD	AWAY
MEAN APPEASEMENT RESPONSE	3.75	1.25	0.0	0.0
S.E.M.	0.5	0.3	0.0	0.0

Table 6B Effect of rotation movements and form of the stimulus on appeasement responses

	STIMULUS CONDITION			
	MODEL MONKEY		CONTROL	
	TOWARD	AWAY	TOWARD	AWAY
MEAN APPEASEMENT RESPONSE	2.9	0.1	0.2	0.03
S.E.M.	0.5	0.07	0.2	0.2

Table 6C No habituation effect on appeasement responses with repeated stimulus testing

	TEST BLOCK			
	1	2	3	4
MEAN APPEASEMENT RESPONSE	1.2	1.1	1.0	0.7
S.E.M.	0.3	0.3	0.2	0.2

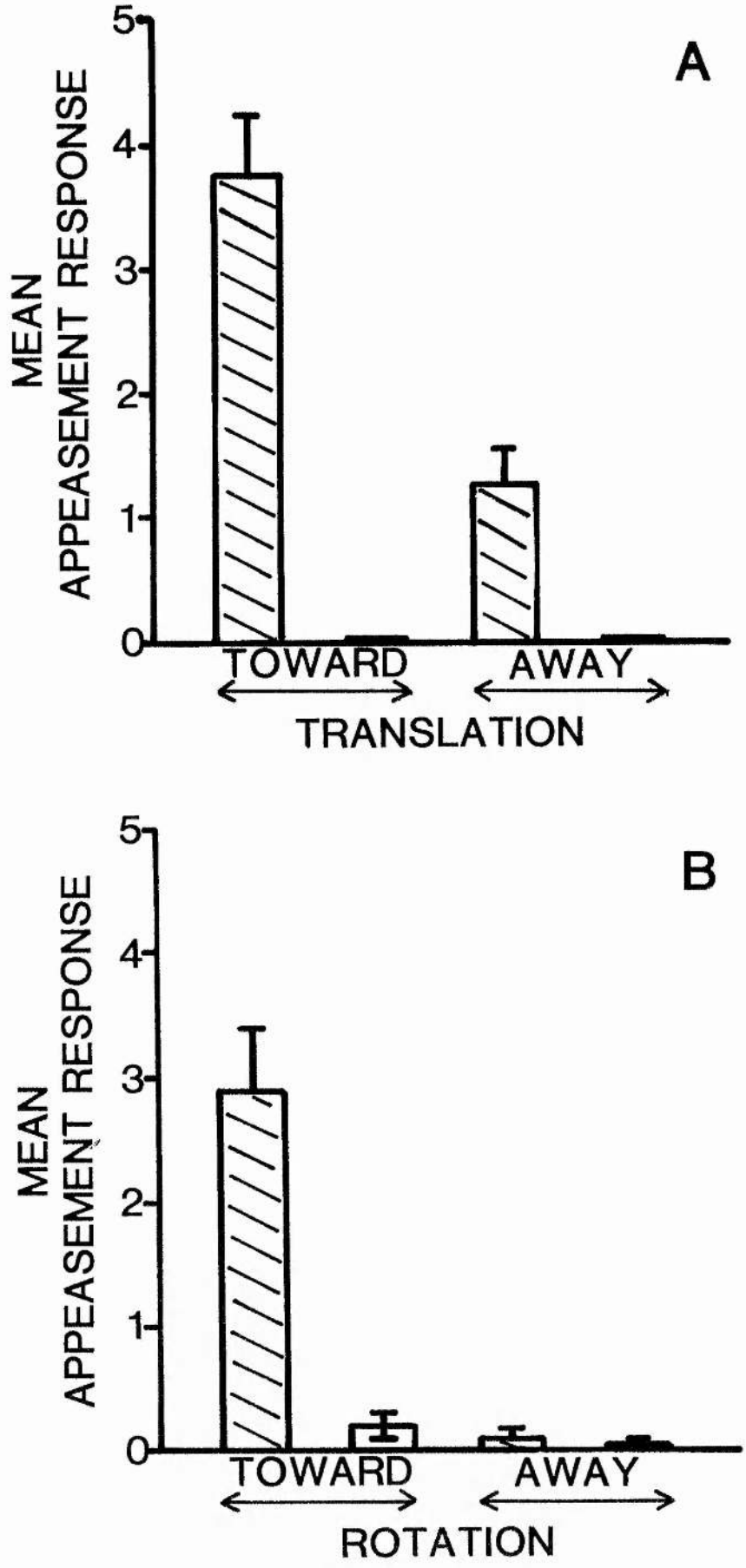


Figure 5.10 Sensitivity to the combined aspects of form and motion. The mean and standard error appeasement response are shown for translation movements towards and away from the viewing monkey (A), and likewise for rotation movements (B). For both figures movements of the model monkey only, towards but not away from the viewing monkey, were strongly appeased. Hatched bar, model monkey stimulus; empty bar, control stimulus.

moving towards the subject (an effective direction of motion) and away from it (an ineffective direction of motion).

(b) Rotations

An identical pattern of responses was observed for the rotation category of movement (Figure 5.10B). Here, a rotation of the model monkey towards the subject (from profile to full face, HoEo pose) elicited a significantly greater response ($p<0.01$) than the model rotating away from the subject (from full face to profile). The model rotating towards the subject also produced a significantly larger response ($p<0.01$) than either movement (rotate towards or away) of the control objects. There was no significant difference between the model rotating away from the subject and the controls rotating in either direction. The response here, as for translations, was dependent on both the form and the motion of the stimulus. The effective stimulus here being a face rotating towards rather than away from the subject. This is comparable to the best response in (a) being elicited by a face translating towards the subject. There was no significant difference in the level of responsiveness these two stimuli produced, i.e. the degree of response did not differ for one or other category of motion.

As for Experiment II, no block effect (or habituation) of responses was observed in this experiment. No significant differences between the mean appeasement responses for each test block, over all conditions (see Table 6C), were noted.

5.4 Discussion

The studies reported here offer an important contribution to methodology in assessing perceptual and emotional responses in monkeys. The employment of 3D stimuli in eliciting social responses is not unique in monkey studies (e.g. Aggleton and Passingham, 1981; Weiskrantz, 1956), but the use of such stimuli specifically designed to represent monkey conspecifics is uncommon. Most often stimuli are chosen arbitrarily, or to represent predators. Testing of social responsivity to conspecifics has been restricted to 2D pictures or videofilm of the behaviour of live monkeys over which an experimenter has too little control. The stimuli used in this study offer such control and emphasize a realistic approach to the behavioural study of primate perceptual functions and emotional responsivity.

5.4.1 Experiment I: Face configuration

The results from Experiment I clearly indicate that models can be used to demonstrate a striking propensity for the facial form, in these monkeys. Resemblance to the face pattern apparently enhances the monkeys' emotional responses triggered by any array of facial features, since the frequency of appeasement responses were reduced for the 3D head models with jumbled features. These results are consistent with Keating and Keating's (1982) findings for two rhesus monkeys that fixation frequencies when scanning objects were enhanced with facelike schematic stimuli and generally reduced for non-facelike

(jumbled) schematic stimuli. Furthermore, the present results parallel those of human infant (pre-verbal) studies, indicating a greater visual interest in facelike rather than non-facelike configurations (e.g. Fagan, 1972; Caron et al, 1973; Haaf, 1977).

The normal arrangement of facial features appeared to be the most important aspect governing responses to the stimuli; yet not all jumbled arrays were treated equally. Perhaps the degree of 'faceness' held by jumbled configurations influences behavioural responses to face-like stimuli. Human ratings of the faceness of these stimuli did not correspond with the rank ordering of monkeys' socio-emotional responses to the stimuli, hence the exact dimensions governing the degree to which an array of facial features are judged as face-like remain unsure.

5.4.2 Experiment II: Head posture

Results from Experiment II demonstrate the monkeys' natural ability to discriminate head postures with respect to the body axis. With the stimulus model monkey's head on a level or lowered with respect to the observing monkey, a large socio-emotional response was elicited; whereas the model monkey's head raised with respect to the observer elicited little or no such response.

A head down posture is characteristic of the non-human primate threat face (Hinde and Rowell, 1962; van Hooff, 1962) and is strongly associated with forward body movements in aggressive gestures or

postures. An observer witnessing such an aggressive threat face (with eyes fixed on the observer, eyebrows raised, ears drawn back against the side of the head, mouth slightly or fully open with lips tensed and upper teeth covered, and body angled forward, i.e. head angled down (van Hooff, 1962)) may act either to confront or appease the aggressor to 'cut-off' any attack response. Submissive or appeasing gestures (such as lipsmacking) by the observer would be a typical display to such a threat posture and may well prevent attack (Hinde and Rowell, 1962; van Hooff, 1962). It is therefore parsimonious to assume that in Experiment II the head down posture of the model stimulus was interpreted as a threat by subjects (observers) who responded appropriately with intense appeasement gesturing. These results are in accord with Sackett's (1965, 1966) observations of a high frequency of submissions and withdrawal responses in rhesus monkeys (notably reared in isolation) to threat pictures. Responses to threatening stimuli in Experiment II occurred despite the absence of the appropriate mouth open component of the complete threat, indicating that individual elements of a compound expression can independently evoke a behavioural response.

The 'normal' posture, HoEo, appeared also to be considered a threatening posture. Possible reasons why this might be so include: The head in normal orientation complete with direct eye contact may typically constitute a threat expression; alternatively, subjects could have perceived the normal orientation as a head down pose because of viewing from a slightly elevated position.

The head up posture is frequently described in the behavioural

repertoire of macaques, but in varying contexts. It has been described as a characterisitic of the submissive or appeasement gestures of lipsmacking and teethchattering where the chin is often raised with respect to the observer (Hinde and Rowell, 1962) and the body angled backward (van Hooff, 1962). Equally, the head is thrown backwards (presenting a head up posture to the onlooker) in yawning (Hinde and Rowell, 1962) where it occurs socially in response to mild stress or in aggressive contexts. The communicative value of yawning has not yet been fully determined, although it has been noted that in agonistic encounters an individual with large canines (made evident in yawning) holds a greater likelihood of emerging victorious in an ensuing fight.

Hinde and Rowell (1962) actually describe a posture related to fear termed 'showing neck'. Here the head is turned up, eye contact with the observer generally removed, the neck elongated and exposed towards the observer. They speculate that this posture functions as an invitation to groom, and as showing submission in aggressive encounters between females, but there has been no assessment of the consequences of individuals adopting this posture. The absence of a discerning socio-emotional response to the head up posture in Experiment II confirms a role for this posture in non-threatening gestures and is compatible with 'head up' being part of a submissive behaviour. Since a normal head posture may be interpreted as threatening then the head up posture could be important in signalling unambiguously the absence of threatening intent.

The manipulation of direct eye gaze and gaze avoidance is an important

channel of communication among monkeys and apes and is a particularly striking feature of primate gestural communication. Scanning or fixation patterns reveal a preoccupation in monkeys for the eyes of stimulus faces, regardless of facial expression (Keating and Keating, 1982); and Bertrand (1969) elaborately described stumptail macaques as 'eye conscious'. Eye gaze can be seen to act as a bonding agent (e.g. Goodall, 1967; Harlow and Mears, 1979) but more often as a threat (e.g. Bertrand, 1969; Hall and DeVore, 1965; Hinde and Rowell, 1962; Scaife, 1976; van Hooff, 1962) which is the context in which the eye signals in Experiment II were expected to act. Eye contact as an element in a compound facial expression is exhibited predominantly by those gestures motivated by a tendency to attack (e.g. threat faces) whereas lateral eye aversion is more commonly associated with gestures motivated by a tendency to flee, or approach with sexual intent (Hinde and Rowell, 1962). A modulation of response to the direction of eye gaze in Experiment II might have been expected, therefore, but it appeared that in this study, the postural head cues were more salient. No differential responsiveness between eye contact and eye aversion was observed for either head up or head down postures. Perhaps eye contact only acted as a threatening cue in the HoEo pose where the threatening nature of the posture was ambiguous.

Mendelson et al (1982) report that monkeys respond emotionally (squirming, squealing and lipsmacking) to pictures of monkeys with eye contact and scan them less than gaze averted pictures, although the eyes were scanned proportionately more for faces with eye contact rather than eye aversion. Similarly, Keating and Keating (1982) found monkeys fixated less on eye averted rhesus faces and more on eye

contact faces. The lack of discrimination reported in Experiment II, in the present study, may arise as a result of the more powerful cue of head posture governing the behavioural response (as already suggested), but alternatively, the eyes may not have been suitably visible in the head up or head down stimulus conditions. In a natural context it is quite feasible that strong illumination by the overhead sun could cast a shadow from the brow ridge over the eyes. In such a situation, calculating the intent of an approaching monkey from an analysis of their gaze direction might be impossible; or if possible, highly risky. Calculation would therefore have to be based on head posture alone, with gaze direction assumed by default to be threatening.

5.4.3 Experiment III: Movement

The results from Experiment III demonstrate the importance of the dynamic aspects of gesturing as not only the static form of the stimulus but also a certain direction of motion of that stimulus can affect the saliency of the gesture. Movements bringing a full-face towards an observer (translate and rotate towards) consistently elicited greater frequencies of appeasement response than movements taking the full-face away (translate and rotate away).

Forward movements of the head and body are characteristic of gestures leading to attack, especially in a threat where the head is jerked toward the object or subject being threatened (Hinde and Rowell, 1962). In response to a threat gesture backing off or turning away

effectively cuts off the attack or threat sequence (Chance, 1962; van Hooff, 1962). From the present study, translations and rotations away from the observer were not perceived as threatening behaviour by the observing monkeys, evoking little or no appeasement response. The lack of emotional response to control objects moving towards the subjects suggests that the monkeys discerned no threat from their approach. These results indicate the necessity for both static and dynamic information about a gesture (form visible during movement, and the direction of movement with respect to the perceiver) to be combined in order to produce an affective response.

5.4.4 Methodological implications

Rarely have real faces or 3-dimensional models of faces been employed in the study of face perception either in humans or monkeys. The unique approach of utilizing a life-size model of a conspecific monkey for a stimulus affords the double benefit of realism with controlled manipulation of the stimulus form. A gesture may have several characteristic components whose association can be documented in the wild, by purely observational studies. But the salience of individual gesture components may be impossible to assess outside of a laboratory where life-like stimuli can be manipulated along single dimensions.

Rosenfeld and van Hoesen (1979) observed habituation in rhesus monkeys of a discriminative response to coloured transparencies of threatening faces. They suggested this was due to the fact that the stimuli were perceived as pictures. Habituation to the monkey head models used as

stimuli in Experiment I was evident over the testing period and comparable to the study above may have been due to the subjects perceiving the stimuli as 'models'. Although 3-dimensional, with colour, contrast and texture, the models were disembodied, i.e. they were only head models and had no internal movement of features. In contrast, the life-sized model of a monkey with flexible joints and eyes proved immensely successful as a stimulus, as no habituation was observed to it.

With Butler's (1961) findings that rhesus monkeys attended motion pictures significantly more than equivalent static photographs of monkey behaviour, endowing the model monkey with more mobility and flexibility should result in an 'ideal' stimulus. Such a model would even better the use of live monkeys where the experimenter has no control over the signals emitted.

The need for social species of primates to identify facial form, and discriminate the threatening and non-threatening head and body postures or postural movements is obvious - considering the importance of gestural communication in primate display. Exploiting stimuli such as those used in the present study may provide the means for further studying the perceptual and emotional reactions of monkeys to such behaviour.

5.4.5 Relation of behavioural studies to neurophysiological studies of the STS

These behavioural findings assume appreciable significance when considered in association with neurophysiological studies (e.g. Chapter 7; Perrett et al, 1984, 1985a,b, 1987a,b; Gross et al, 1972) of an area of the macaque temporal lobe, the superior temporal sulcus (STS). In this area, small populations of cells have been identified sensitive to those face and body attributes that were investigated in the behavioural studies. Of concern are four independent populations of cells sensitive to: The configuration of facial features; specific head postures including head up and head down; eye position in the vertical plane; and movements towards and away from the observing monkey.

(a) Configuration of facial features

In direct comparison with Experiment I of this study, three out of four cells were noted to give a greater response to features of a photographed face in normal configuration than to these features jumbled (with or without symmetry) within the hair outline of the face form (Gross et al, 1972; Perrett et al, 1982). These authors additionally observed that only one cell gave a large and consistent response to the 2D face with appropriate configuration of features, this response being elicited more frequently by real 3D faces. (It is of interest to note that, even at the single cell level, a preference for more lifelike stimuli is evident.) Facial components, e.g. restricted facial views such as the hair and forehead, the eye region or the lower half of the face below the eyes, were less effective than full face pictures in eliciting a response in face-sensitive cells too (Perrett et al, 1984). Thus cells sensitive to visual information present in faces were less sensitive to patterns that didn't possess

normal organization of facial features and relied on a combination of different regions.

It would appear that the studies at the behavioural level on the perception of face configuration reflect the neural sensitivity described here. If the STS controls the mechanisms by which affective behaviour is affiliated to certain stimuli or events (see Chapter 7 for a fuller discussion) then these neurones may form the visual basis for the behavioural discriminations observed between normal and jumbled arrays of facial features.

(b) Head postures

Perrett et al (1985b) observed 18 cells (nearly 10% of the cells selectively responsive to the face and head) in the macaque STS sensitive specifically to head orientation in the vertical plane, not the horizontal plane. Eight cells responded preferentially to the head oriented up (chin raised 45 degrees), giving little or no response to the head down, a frontal face or profile. Correspondingly eight cells responded to the head down (chin lowered 45-90 degrees). Two cells were responsive more to the head oriented either up or down than full face. These cells sensitive to vertical head orientation tended to generalize across the horizontal view of the head, e.g. these cells could respond to either the frontal or profile face with the head lowered or raised. Perrett et al (1985b) concluded that these cells were tuned to multiple visual cues.

Only six specific head views appear to be coded by the cells in the STS: Frontal face; left profile; right profile; back of head; head

up; and head down. No cells appear maximally tuned to the head oriented at an angle between these views so Perrett et al (1984, 1985b) classed these orientations as 'prototypical' views of the head. Head up and head down views may be thought of as subclasses of the other prototypical views since neurones sensitive to both profile head down and full face head down have been encountered. The differential behavioural responses to the head up and head down postures observed in Experiment II, however, seem to justify the inclusion of these head orientations as prototypical views. Again, as for face configuration, the behavioural responsivity seems to reflect the neural activity in the STS. Such neurones coding head orientation may provide the perceptual input to a system organizing appropriate affective responses to these socially relevant stimuli.

(c) Eye position in the vertical plane

Gaze direction in the vertical plane has not been widely investigated but a small population of neurones have been identified sensitive to the head up posture with gaze averted from the viewing monkey (Perrett et al, 1985b). Five out of seven cells responding to the head rotating up were found to respond, independent of head position, to gaze directed up. Another five cells were sensitive to both the vertical and the horizontal position of the eyes, preferring eye contact with full face and eyes averted either upwards or laterally with the face rotated away from the observing monkey either up, down, left or right.

Discrimination of gaze direction at the cellular level was not paralleled by the behavioural results of Experiment II. Here no

response differentiation was observed for different eye gaze directions implying that either the response measure was insensitive to this dimension, or that this dimension was not used as a behavioural cue in the context of the experimental situation. Considering the behavioural results alone, one could be misled over the importance of gaze direction in social communication. But by combining the behavioural approach with that of a neurophysiological one a very different interpretation of the findings is available.

(d) Movements towards and away from the monkey

Perrett et al (1985a) describe a number of cell populations sensitive to movements along three orthogonal axes - up/down, left/right, and towards/away. In the latter direction four separate populations of cells have been identified (Perrett et al, 1985a) sensitive to: Translate (but not rotate) towards (39 cells), translate away (22 cells), rotate (but not translate) towards (31 cells), and rotate away (22 cells). Of the motion-sensitive cells, 75% were form selective, i.e. sensitive to movement of the whole, or part of a, body moving in the preferred direction. Perrett et al (1985a) conclude that one functional reason for conjoint form and motion sensitivity in the nervous system is to characterize social expressions. An obvious example described is for faces and bodies rapidly approaching the monkey, since these looming or lunging movements can indicate threatening behaviour.

This reasoning seems accurate considering the behavioural evidence from Experiment III. Appeasement gestures are elicited only by movements towards an observing monkey (both rotate and translate) of a

socially meaningful stimulus, (a model of) another monkey. No distinction at the behavioural level was made between translate and rotate towards which suggests that functionally these two movements are not dissimilar (bringing a face towards the observing monkey). But their visual transformations are distinct and require separate neuronal analysis in the STS. Bringing together these channels of visual information processing, (a function of the STS?), may result in these types of movement coming to have identical social implications.

This neurophysiological data fits hand in hand with the behavioural data presented here and presses for a more multidisciplinary approach to this aspect of psychological research. The culmination of this work lies in testing STS lesioned monkeys on these behavioural tasks, to see whether these neurones do provide input to an affect system, controlling responses observed to biologically meaningful stimuli.

5.5 References

Aggleton, J.P., and Passingham, R.E. (1981) Syndrome produced by lesions of the amygdala in monkeys (Macaca mulatta). J. Comp. Physiol. Psychol. 95:961-977.

Anisfeld, M. (1979) Interpreting "imitative" responses in early infancy. Science 205:215.

Bertrand, M. (1969) The behavioural repertoire of the stumptail macaque. Bibliotheca Primatologica no.11. Karger, Basel.

Boothe, R.G., Kiorpes, L., Regal, D.M., and Lee, C.D. (1982) Development of visual responsiveness in Macaca nemestrina monkeys. Dev. Psychol. 18:665-670.

Bushnell, I. (1983) Born to see. New Scientist 100:816-818.

Butler, R.A. (1961) The responsiveness of rhesus monkeys to motion pictures. J. Gen. Psychol. 98:29-245.

Caron, A.J., Caron, R.F., Caldwell, R.C., and Weiss, S.J. (1973) Infant perception of the structural properties of the face. Dev. Psychol 9:385-399.

Chalmers, N.R. (1979) Social behaviour in Primates. Edward Arnold Ltd, London.

Chance, M.R.A. (1962) An interpretation of some agonistic postures: The role of "cut-off" acts and postures. Symp. zool. Soc. Lond. 8:71-99.

Chevalier-Skolnikoff, S. (1974) The ontogeny of communication in the stumptail macaque (Macaca arctoides). In: H. Kuhn, and A.H. Schultz (eds) Contributions to Primatology, vol.2. Karger, Basel, pp.55-99.

Fagan, J.F. (1972) Infants' recognition memory for faces. J. Exp. Child Psychol. 14:453-476.

Fantz, R.L. (1961) The origin of form perception. Sci. Am. 204:66-72.

Fantz, R.L. (1963) Pattern vision in newborn infants. Science 140:296-297.

Field, T.M., Woodson, R., Greenberg, R., and Cohen, D. (1982) Discrimination and imitation of facial expressions by neonates. Science 218:179-181.

Foley, J.P.Jr. (1934) First year development of a rhesus monkey (Macaca mulatta) reared in isolation. J. Gen. Psychol. 45:39-105.

Goodall, J. van Lawick (1967) Mother-offspring relationships in free-ranging chimpanzees. In: D. Morris (ed) Primate Ethology. Weidenfeld and Nicholson, London.

Goren, C.G., Sarty, M., and Wu, P.Y.K. (1975) Visual following and pattern discrimination of face-like stimuli by newborn infants. Pediatrics 56:544-549.

Gross, C.G., Rocha-Miranda, E.E., and Bender, D.B. (1972) Visual properties of neurons in inferotemporal cortex of the macaque. J. Neurophys. 35:96-111.

Haaf, R.A. (1977) Visual response to complex facelike patterns by 15- and 20- week old infants. Dev. Psychol. 13:77-78.

Haaf R.A., and Bell, R.Q. (1967) A facial dimension in visual discrimination by human infants. Child Dev. 38:893-899.

Hainline, L. (1978) Developmental changes in visual scanning of face and non-face patterns by infants. J. Exp. Child Psychol. 25:90-115.

Haith, M., Bergman, T., and Moore, M. (1977) Eye contact and face scanning in early infancy. Science 198:853-855.

Hall, K.R.L., and DeVore, I. (1965) Baboon social behaviour. In: I. DeVore (ed.) Primate Behaviour: Field Studies of Monkeys and Apes. Holt, Rinehart and Winston, New York, pp.53-110.

Harlow, H.F., and Mears, C. (1979) The Human Model: Primate Perspectives. John Wiley, New York.

Hinde, R.A., and Rowell, T.E. (1962) Communication by postures and facial expressions in the rhesus monkey (Macaca mulatta). Proc. zool. Soc. Lond. 138:1-21.

Humphrey, N.K. (1974) Species and individuals in the perceptual world of monkeys. Perception 3:105-114.

Jacobson, S.W., and Kagan, J. (1979) Interpreting "imitative" responses in early infancy. Science 205:215-217.

Kagan, J., Henker, B., Hen-Tov, A., Levine, J., and Lewis, M. (1966) Infant's differential reactions to familiar and distorted faces. Child Dev. 37:519-532.

Keating, C.P., and Keating, E.G. (1982) Visual scan patterns of rhesus monkeys viewing faces. Perception 11:211-219.

Kenney, M.D., Mason, W.A., and Hill, S.D. (1979) Effects of age, objects and visual experience on affective responses of rhesus monkeys to strangers. Dev. Psychol. 15:176-184.

Koopman, P., and Ames, E.W. (1968) Infant's preferences for facial arrangements: A failure to replicate. Child Dev. 39:481-487.

Masters, J.C. (1979) Interpreting "imitative" responses in early infancy. Science 205:215.

Maurer, D., and Barrera, M. (1981) Infants' perception of natural and distorted arrangements of a schematic face. Child Dev. 52:196-202.

Maurer, D., and Salapatek, P. (1976) Developmental changes in scanning of faces by young infants. Child Dev. 47:523-527.

Meltzoff, A.N., and Moore, M.K. (1977) Imitation of facial and manual gestures by human neonates. Science 198:75.

Meltzoff, A.N., and Moore, M.K. (1979) Interpreting "imitative" responses in early infancy. Science 205:217-219.

Meltzoff, A.N., and Moore, M.K. (1983) Newborn infants imitate adult facial gestures. Child Dev. 54:702-709.

Mendelson, M.J. (1982) Clinical examination of visual and social responses in infant rhesus monkeys. Dev. Psychol. 18:658-664.

Mendelson, M.J., Haith, M.M., and Goldman-Rakic, P.S. (1982) Face scanning and responsiveness to social cues in infant rhesus monkeys. Dev. Psychol. 18:222-228.

Overman, W.H. Jr, and Doty, R.W. (1982) Hemispheric specialization displayed by man but not by macaques for analysis of faces. Neuropsychologia 20:113-128.

Perrett, D.I., Harries, M., Mistlin, A.J., and Chitty, A.J. (1987a) Three stages in the classification of body movements by visual neurons. In: H. Barlow, C. Blakemore and M. Weston Smith (eds) Images and Understanding. Cambridge University Press, Cambridge (in press).

Perrett, D.I., Mistlin, A.J., and Chitty, A.J. (1987b) Visual neurones responsive to faces. Trends Neurosci. 10:358-364.

Perrett, D.I., Rolls, E.T., and Caan, W. (1982) Visual neurones responsive to faces in the monkey tempral cortexx. Exp. Brain Res. 47:329-342.

Perrett, D.I., Smith, P.A.J., Mistlin, A.J., Chitty, A.J., Head, A.S., Potter, D.D., Broennimann, R., Milner, A.D., and Jeeves, M.A. (1985a) Visual anlysis of body movements by neurones in the temporal cortex of the macaque monkey: A preliminary report. Behav. Brain Res. 16:153-170.

Perrett, D.I., Smith, P.A.J., Potter, D.D., Mistlin, A.J., Head, A.S., Milner, A.D., and Jeeves, M.A. (1984) Neurones responsive to faces in the temporal cortex: Studies of functional organization, sensitivity to identity and relation to perception.

Human Neurobiol. 3:197-208.

Perrett, D.I., Smith, P.A.J., Potter, D.D., Mistlin, A.J., Head, A.S., Milner, A.D., and Jeeves, M.A. (1985b) Visual cells in the temporal cortex sensitive to face view and gaze direction. Proc. roy. Soc. Lond. B 223:293-317.

Premack, D. (1975) Putting a face together. Science 188:228-236.

Rosenfeld, S.A., and van Hoesen, G.W. (1979) Face recognition in the rhesus monkey. Neuropsychologia 17:176-186.

Sackett, G.P. (1965) Response of rhesus monkeys to social stimulation presented by means of coloured slides. Percept. Mot. Skills 20:1027-1028.

Sackett, G.P. (1966) Monkeys reared in isolation with pictures as visual input: Evidence for an innate releasing mechanism. Science 154:1470-1473.

Salapatek, P. (1975) Pattern perception in early infancy. In: L.B. Cohen, and P. Salapatek (eds) Infant Perception: From Sensation to Cognition. Academic Press, New York, pp.138-248.

Scaife, M. (1976) Response to eye-like shapes by birds II: Importance of staring, pairedness and shape. Anim. Behav. 24:200-206.

Spieker, S. (1982) Infant recognition of invariant categories of faces: Person identity and facial expression. PhD Thesis, Cornell University.

van Hooff, J.A.R.A.M. (1962) Facial expressions in higher primates. Symp. zool. Soc. Lond. 8:97-125.

Weiskrantz, L. (1956) Behavioural changes associated with ablations of the amygdaloid complex in monkeys. J. Comp. Physiol. Psychol. 49:381-391.

Wu, H.M.H., Holmes, W.G., Medina, S.R., and Sackett, G.P. (1980) Kin preference in infant Macaca nemestrina. Nature 285:225-227.

CHAPTER 6

Evaluation of the effects of superior temporal sulcus lesions on monkeys' behavioural responses to socially relevant stimuli.

6.1 Introduction

The bilateral destruction of the temporal lobes (including both the cortical structures and the amygdala) in monkeys, produces a complex set of symptoms that are collectively referred to as the Kluver-Bucy syndrome (Kluver and Bucy, 1939). Monkeys with such lesions manifest difficulties in visual discrimination tasks. Also, they are unable visually to differentiate the significance of objects from their visual appearance; examine objects excessively - often orally; will eat previously rejected items such as meat or faeces (coprophagia); react compulsively to stimuli (hypermetamorphosia); appear emotionally unresponsive; and may become hypersexual. Little effort has been made to distinguish whether these symptoms arise from the same impairment or whether selective lesions within the ablated regions could be responsible for specific components of the syndrome. An obvious question to ask, therefore, is whether the components of the Kluver-Bucy syndrome are dissociable.

It is accepted from the numerous studies of the effects of amygdalectomy on social and non-social behaviour that removal of the amygdala alone can produce the majority of behavioural changes noted with conjoint temporal neocortex and amygdala lesions (Aggleton and

Passingham, 1981; Dicks et al, 1969; Gloor, 1960; Goddard, 1964; Horel et al, 1975; Kling, 1972; Mishkin and Aggleton, 1981; Rosvold et al, 1954; Thompson and Towfighi, 1976; Thompson et al, 1969, 1977; Weiskrantz, 1956). Similarly, removal of the temporal neocortex, sparing the amygdala, results in the expression of most symptoms of the behavioural syndrome (Horel et al, 1975; Myers and Swett, 1970).

Further attempts to fractionate the Kluver-Bucy syndrome have revealed that ablation of the middle and inferior gyri (the inferotemporal cortex) result in the deficits in visual discrimination described with total temporal lobe lesions (Cowey and Gross, 1970; Iwai and Mishkin, 1969; Mishkin, 1954), i.e. in deficits of performance on learned visual problems. These visual discrimination deficits are not generally seen, however, after amygdala damage (Aggleton and Passingham, 1981; Mishkin, 1954; Schwartzbaum, 1965; Weiskrantz, 1956). Since the visual discrimination deficits that follow damage to the inferotemporal cortex are not seen after amygdala damage but the other symptoms are, it has been claimed that the amygdala is the source of behavioural deficits in Kluver-Bucy syndrome (Gloor, 1960; Goddard, 1964).

Aggleton and Passingham (1981) investigated the behavioural effects of subtotal amygdaloid lesions, looking to dissociate some of the abnormalities seen after total amygdalectomy. They found that the monkeys with subtotal lesions exhibited no food preference changes but were more willing to approach and investigate animate and inanimate objects more than control animals. Some small changes in emotionality were observed for these animals who tended to show high levels of

submissive behaviour. But in contrast, the animals with total amygdaloid lesions ate meat or faeces (previously avoided) and handled more inedible objects than control animals, exhibited excessive exploration behaviour and were hypoemotional. An impairment on serial reversal object discrimination was observed only for those animals with large or complete amygdaloid lesions. From this evidence Aggleton and Passingham (1981) concluded that it is necessary to remove all of the 'visual' termination regions within the amygdala to produce the full "disconnection" syndrome.

Information about the environment is processed in stages from the sense receptors through the primary and secondary sensory cortices to the association areas of the brain, e.g. the temporal neocortex. The next stage of processing is postulated to be the limbic system which is proposed to associate stimuli with motivational or emotional significance (Geschwind, 1965; Jones and Mishkin, 1972; Weiskrantz, 1970). The amygdala has been implicated as one of these relevant limbic structures. Now it has been suggested that the Kluver-Bucy syndrome results from a disconnection of the sensory analysis of stimuli from affective qualities (Geschwind, 1965; Jones and Mishkin, 1972). From this it seems clear that by damaging the limbic structures involved or removing the appropriate sensory input from this structure, behavioural symptoms of Kluver-Bucy would be produced. The effect of removing specific visual inputs to the amygdala from particular subregions of the temporal neocortex has not been fully explored.

The superior temporal sulcus (STS) projects heavily to the amygdala

(Aggleton et al, 1980; Jones and Powell, 1970) supplying this structure with, as yet, an undefined channel of information. Physiological data from single-unit recording studies of the STS (Bruce et al, 1981; Gross et al, 1981; Perrett et al, 1984, 1985a,b; and see Chapters 4 and 7) demonstrate this area's involvement with the coding of complex stimuli that have some biological significance to the monkey. Populations of visual cells have been identified sensitive specifically to faces (face view and expressions) and other parts of the body (body view and posture), which could be coding features and gestures important in social behaviour. Somatosensory sensitive cells in the STS show a remarkable sensitivity only to types of tactile stimuli to which some form of affective response may need to be attached (Chapter 4).

From these findings it might be suggested that the STS is performing a high-level analysis of socially relevant stimuli. Thus, the STS may be of special importance to the amygdala as the visual input for sensory information relating directly to social communicative behaviour. Consequently selective damage to the STS may affect the ability of monkeys to respond appropriately to certain social stimuli, so giving rise to one of the major behavioural symptoms of the Kluver-Bucy syndrome.

The success of experimental methods described in Chapter 5 in revealing natural discriminatory responses in monkeys to distinct face and body attributes, presumed important in social communication, led to their direct adaptation for studying STS-damaged monkeys.

6.2 General Methods

This section describes the similar techniques, to those in Chapter 5, used to investigate both unoperated and superior temporal sulcus (STS) lesioned monkeys' natural capacity to discriminate certain facial and body attributes. The investigation of differential responsiveness of monkeys to the correct and jumbled arrangements of facial features, and to head postures and direction of eye gaze (Experiments I and II respectively in Chapter 5) correlate directly with Experiments I and II in this chapter. The experimental design and the stimuli used are identical to those described previously; but due to a different testing location slight variations in the apparatus and procedure must be reported. Additionally, a more detailed anlaysis of behavioural responses was employed.

I am indebted to Professor Alan Cowey and Dr Charles Heywood for the extended use of their testing facilities in the Department of Experimental Psychology at the University of Oxford; and for supplying the subjects for the following experiments. The lesions were performed by Professor Cowey and are reported in Heywood and Cowey (1987). For direct comparison with those experiments of the previous chapter and for ease of exposition, the descriptions (where dissimilar) and results of the two experiments are reported separately.

6.2.1 Subjects

Six adult rhesus monkeys (Macaca mulatta) and two cynomolgus monkeys (Macaca fascicularis) were used in this study. Both the experimental and control subjects were part of ongoing studies in Oxford. As the surgery was performed as part of the Oxford studies, not previously intended for the studies reported here, the opportunity to match subjects for species, sex, age or weight, or pre-operative experience was limited.

Two experiments were carried out on animals previously assigned to the non-surgical (control) or the surgical group (STS). In the first series of experiments, postoperative socio-emotional responsivity was assessed in three STS-lesioned monkeys (Group STS) and three unoperated control animals, two rhesus and one cynomolgus per group. In the second series of experiments two of the rhesus monkeys that served as unoperated controls received lesions that provided additional animals for the experimental group. Two naive rhesus monkeys acted as unoperated controls here.

Monkeys were maintained in a healthy condition and received a diet of commercial chow, fruit and vitamin supplements. They were generally given their daily feed shortly after testing. The subjects were all housed separately but within sight of their peers.

6.2.2 Surgery

The surgical procedure employed by Professor Cowey is reported in Heywood and Cowey (1987). Suffice to say, ablations were bilateral

and made at a single operation by sub-pial aspiration. All animals recovered promptly and uneventfully from the surgery and behavioural testing of these animals proceeded 11-12 months after surgery for animals STS1, STS2 and STS3; and 4 months for STS4 and STS5.

6.2.3 Histology

Histological details are also given in Heywood and Cowey (1987), where the lesion sites of the STS ablated monkeys (used in these experiments) are presented.

6.2.4 Stimuli

The stimuli used for Experiments I and II are described in Section 5.2.2, in the corresponding sections.

6.2.5 Apparatus

All testing was carried out in a Wisconsin General Testing Apparatus (WGTA) in the presence of masking white noise. (The basic WGTA design followed that shown in Figure 5.4.) The compartment in which stimuli were presented was 75cm wide, 75cm high and 45cm deep and lined with black cardboard. It was illuminated by three fluorescent lamps (Thorn, Artificial Daylight). Two lamps were positioned vertically at the front and at each side of the compartment, the third placed

horizontally at the top, and a fourth placed directly above the animal's transport cage in such a position as to cast only direct light on to the stimuli. These arrangements avoided the animal being able to see its own reflection and prevented uneven light being shed on the stimuli.

The subjects' behavioural responses over the test period were continuously filmed by a Canon VC-20 colour video camera positioned discreetly behind the screen at the rear of the compartment. In Experiment I this screen was replaced with a sheet of black perspex in which a rectangle 10cm by 9cm had been removed from the top right hand corner of the screen to enable filming of the monkeys' responses. In Experiment II a black material backdrop covering extraneous cues present behind the stimuli, encompassed the body of the camera so that only the lens was visible and able to film, unseen, the monkeys' behaviour.

The data was recorded on a Panasonic VHS portable video cassette recorder to provide a permanent record of performance. A video monitor (Sony VFA 0014) connected directly to the video camera aided monitoring of the subject's attention during and between testing.

(a) Experiment I: Face configuration

A board, 45cm by 20cm, on which the stimuli rested was mounted on a wheeled trolley which, by means of a handle (22cm long) projecting through the screen at the rear of the compartment, could be pushed along fixed metal tracks directly towards and away from the animal in the transport cage.

(b) Experiment II: Head posture

The stimulus was secured in a neutral posture to a seat placed at the rear of the compartment. The stimulus was placed approximately 1m from the subject with the model's head at the subjects' eye level.

6.2.6 General procedure

Procedure was identical to that described in section 5.2.4. Except, the subjects were transferred from individual cages to the transport cage, rather than from a colony.

6.2.7 Stimulus presentation

An accurate description of this is given in section 5.2.5. One notable variation was that the separate experiments had to be performed just one to two days apart as these animals were required to perform in other tasks. Additionally for Experiments I and II, the presentation time for each stimulus trial was reduced to two seconds.

6.2.8 Response measures and data collection

A socio-emotional index was compiled (from Aggleton and Mishkin, 1983 and Horel et al, 1975) classifying the behavioural responses into two deferential categories, attack and submission. Table 7 lists the individual elements of the responses and indicates the arbitrary index

Table 7 Socio-Emotional Response Index (S.E.R.I.) Scores

Category	Element	Score
Attack	Full mouth threat	2
	(or Half open mouth	1)
	Head and/or body lunge	1
	Direct stare	1
	Cage shake	0.5
	Strike	0.5
Appeasement	Lipsmack >10	5
	Lipsmack 7-10	4
	Lipsmack 4-6	3
	Lipsmack 2-3	2
	Lipsmack 1	1

scores assigned to them. (In the appeasement category lipsmack only is indicated, but note that lipsmacking and teethchattering were treated equally.) A maximum score of five was possible for the strongest response in each category, which were not mutually exclusive.

The change in scoring of the response measure was necessary because rhesus and cynomolgus macaques utilize different behavioural repertoires to those of the stumptail macaques.

In the attack category the scores were graded according to the frequency with which the response elements are commonly observed. The total score in the threat category equalled the sum of the scores of the individual elements comprising the total threat gesture (=5). In the submissive category the highest possible frequency of appeasement gesturing was awarded the highest score, 5, (on a par with the complete threat response score), then a sequential decrease in response rewarded a comparitively decreased score.

The data collected on the videotapes were transcribed onto data sheets, the presence of any of the defined response elements noted, and an appropriate score assigned. Other behavioural responses including vocalizations and uncategorized gestures (e.g. chewing, teeth grinding) were noted but not scored.

6.3 RESULTS

6.3.1 Histology

In the lesioned animals (Group STS) an attempt was made to remove the area of the STS cortex containing cells responsive to faces. The STS ablation included both banks of the sulcus for a length of about 15mm, starting approximately 5mm in front of the tip of the inferior occipital sulcus. In addition, as much as possible of the floor of the sulcus within this region was removed where this could be done without damaging major vessels or encroaching on white matter including the visual radiations. Two rhesus monkeys (STS1 and STS2), however, received only a unilateral STS lesion. In these animals a comparable ablation was made a few millimetres rostral and dorsal to the first one but in the sylvian sulcus of the opposite hemisphere (Heywood and Cowey, 1987).

Had more rigid control over the experimental design of the study been possible, a more balanced lesion group would have been obtained.

6.3.2 Experiment I: Face configuration

For both experiments the general pattern of responsivity generated by each experimental group is presented prior to a comparison of performance (measured on the socio-emotional response index) between pre-operative and post-operative animals.

Table 8A shows for each experimental group the mean socio-emotional response index (S.E.R.I.) score and standard error per stimulus

condition. These scores were calculated from each individual's mean score in that group; this included the scores of those animals which appear in both groups. Statistical analysis of these data are included as a helpful means by which to observe changes in the animals' behaviour.

A 5 (subject) X 4 (test block of trials) X 6 (condition) one-way analysis of variance (ANOVA) on the unoperated control group suggested a main condition effect, $F(5,20)=5.09$, $p<0.01$. Post hoc analysis suggested that the normal head model, N, elicited a significantly greater response than J2 ($p<0.05$ Newman-Keuls), J2 having rated the highest behavioural score of the jumbled face models (illustrated in Figure 6.1). Both N and J2 elicited a significantly greater response than the control objects ($p<0.01$ and $p<0.05$ respectively). An ANOVA of the STS group also revealed a main condition effect, $F(5,20)=4.63$, $p<0.01$. All the head models, regardless of the facial feature array, produced a response greater than that to the control objects ($p<0.05$ each comparison). However, no significant differences were observed between the head models, contrary to that seen for the unoperated control animals (see also Figure 6.1).

Table 8B indicates the mean S.E.R.I. scores pre-operatively and post-operatively for two subjects, Wellington (UNOP1/STS4) and Plugg (UNOP2/STS5). For Wellington (Figure 6.2A) an ANOVA revealed a pre/post-operative X condition interaction effect, $F(5,15)=10.44$, $p<0.001$. Further analysis of the pre-operative data showed a significant condition effect, $F(5,15)=14.1$, $p<0.0001$. The normal head model, N, elicited a significantly greater response than any of the

Table 8A Overall effect of STS ablation on socio-emotional responses to face configuration

	STIMULUS CONDITION					
SUBJECT GROUP	N	J1	J2	J3	B	C
UNOPERATED	3.12 +/-0.5	1.67 +/-0.4	1.75 +/-0.4	1.57 +/-0.4	1.0 +/-0.3	0.23 +/-0.07
STS LESION	1.76 +/-0.4	1.42 +/-0.3	1.77 +/-0.3	2.12 +/-0.3	1.25 +/-0.4	0.31 +/-0.08

Table 8B Effect of STS-lesion surgery on socio-emotional responses to face configuration

	STIMULUS CONDITION					
SUBJECT GROUP	N	J1	J2	J3	B	C
UNOPERATED WELLINGTON	4.4 +/-1.0	0.75 +/-0.5	0.75 +/-0.2	0.5 +/-0.5	0.5 +/-0.3	0.6 +/-0.3
STS LESION WELLINGTON	0.5 +/-0.3	0.1 +/-0.1	1.0 +/-0.4	1.7 +/-0.7	0.2 +/-0.2	0.4 +/-0.1
UNOPERATED PLUGG	2.2 +/-1.0	1.1 +/-1.1	0.7 +/-0.2	1.1 +/-0.5	0.7 +/-0.2	0.1 +/-0.05
STS LESION PLUGG	0.1 +/-0.1	0.1 +/-0.1	0.1 +/-0.1	0.6 +/-0.5	0.0 +/-0.0	0.1 +/-0.06

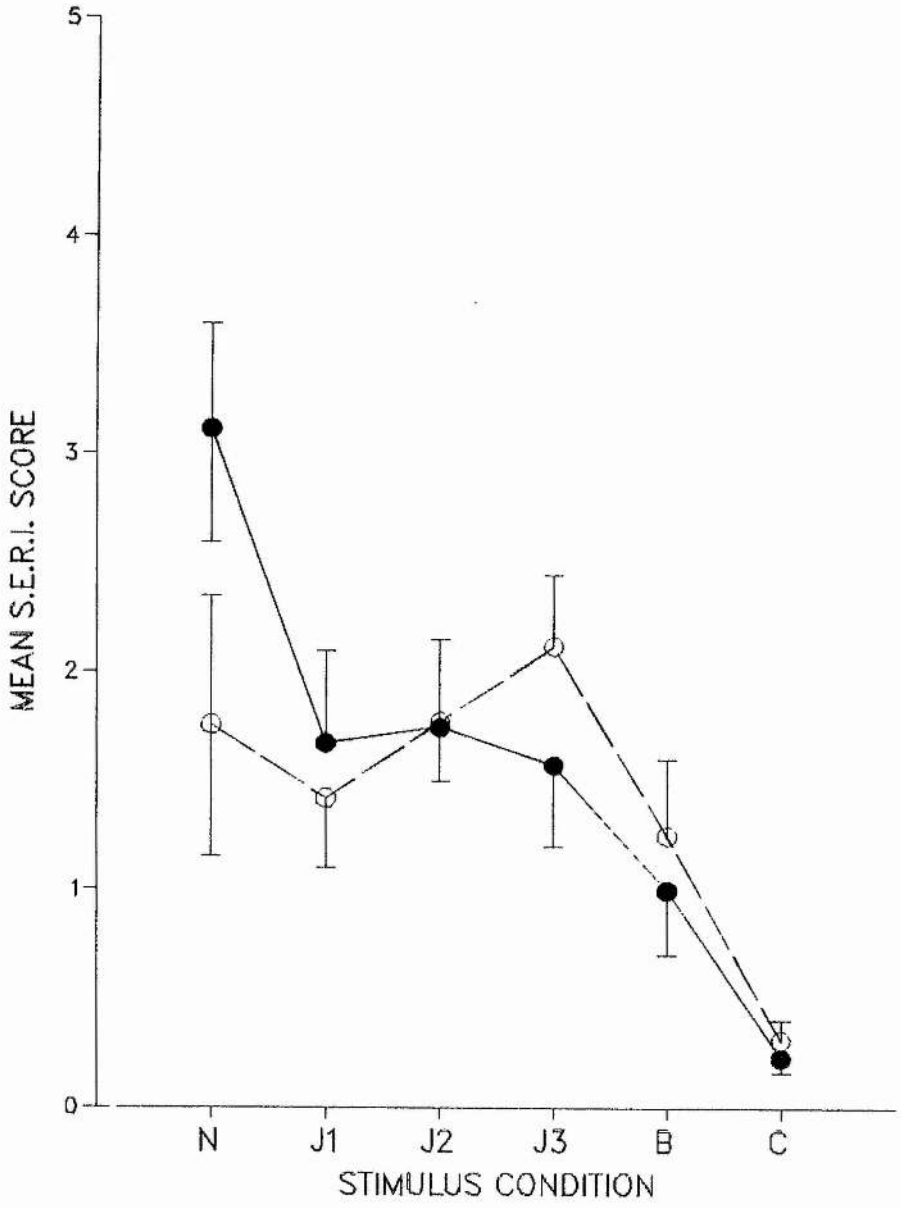


Figure 6.1 Overall effect of STS ablation on sensitivity to facial configuration. Socio-emotional response index (S.E.R.I.) scores indicated the inability of the STS-lesioned animals (but not the unoperated animals) to discriminate between the stimulus with normal face configuration (N), and the stimuli with jumbled features (J1-J3), no internal features (B), and the non-face controls. Filled circle/solid line, unoperated group; open circle/dashed line, STS-lesioned group. (Non-overlapping error bars only are shown.)

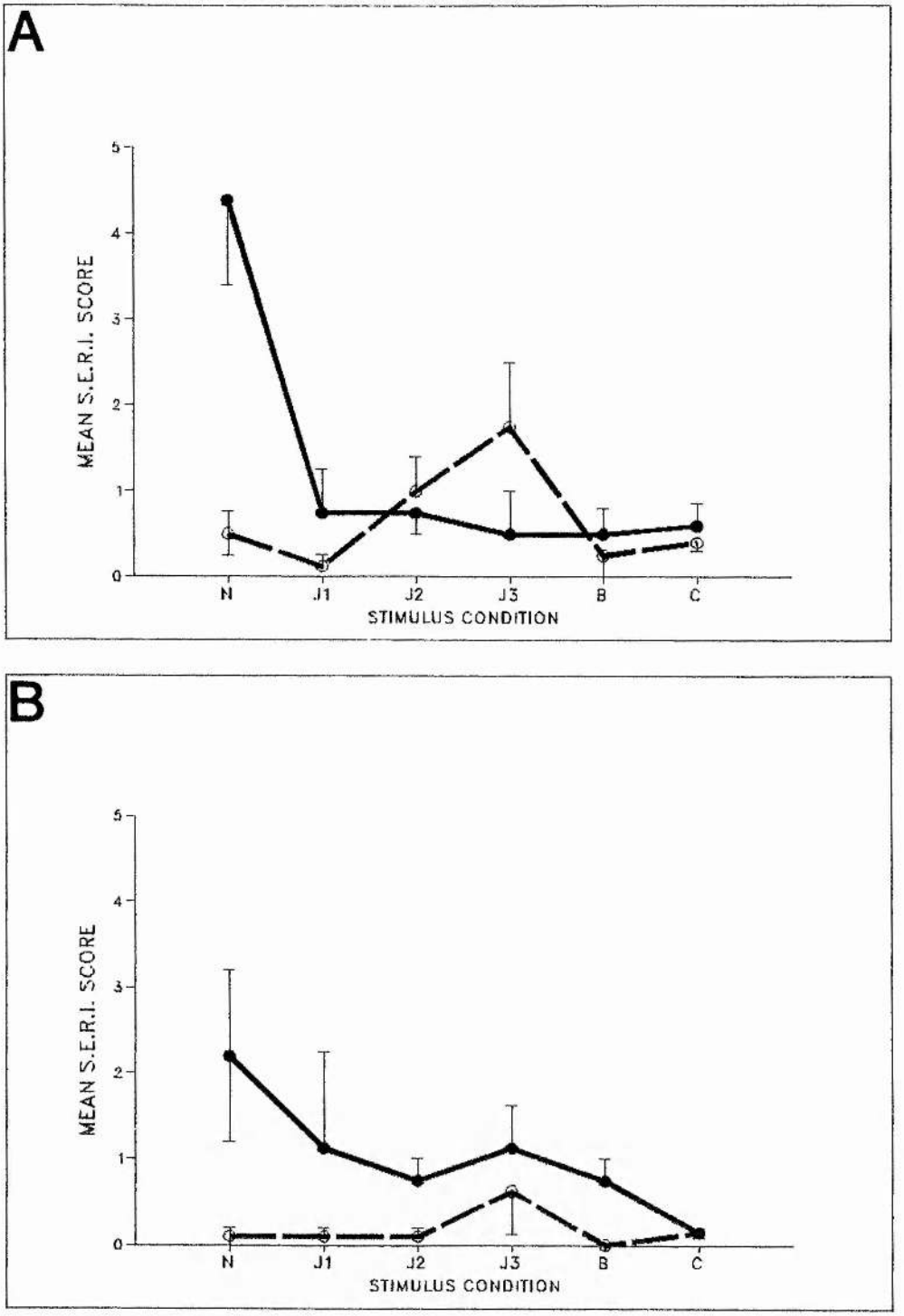


Figure 6.2 Effect of STS ablation surgery on sensitivity to facial configuration in two monkeys. Comparison of pre- and post-operative performance (measured by the S.E.R.I.) for both Wellington (A) and Plugg (B) indicates a reduced sensitivity to the normal face configuration (N) post-operatively. Filled circle/solid line, pre-operative; open circle/dashed line, post-operative.

other head models or the control objects ($p<0.01$ Newman-Keuls (N-K) each comparison); no other significant differences were observed. In direct contrast, analysis of the post-operative data revealed no significant condition effect. Pair comparison of pre/post-operative scores then showed a significant difference only for the normal head model, N ($p<0.05$).

For Plugg (Figure 6.2B) an ANOVA revealed no pre/post-operative X condition interaction. Nevertheless comparison of the two animals does seem to suggest the same pattern of behaviour, that of a decrease in responsivity from N to the jumbled models pre-operatively and lack of discrimination between the models post-operatively.

In summary, the unoperated control animals appeared to be most responsive to the normal head model, whereas the STS group of animals displayed no such discrimination between the models. The STS group did seem able to discriminate between the models and the control objects. This behavioural pattern was in essence paralleled by both of the animals tested pre- and post-operatively on the face configuration experiment.

6.3.3 Experiment II: Head posture

Table 9A shows for each experimental group the mean S.E.R.I. score and standard error per stimulus condition (as for Table 8A, Experiment I). These scores were again calculated from each individual's score in that group. The unoperated control group contained three animals

and the STS group, five animals. Scores for the pre- and post-operatively tested animals were included as part of the group scores. The collected data are illustrated in Figure 6.3.

An ANOVA for the STS lesioned animals revealed a significant stimulus condition effect where $F(5,20)=4.19$ and $p<0.01$. Post hoc analysis showed no significant differences between the head postures but did show that all the head postures elicited significantly greater behavioural scores than the control objects ($p<0.05$ N-K each comparison, except HoEo > C, $p<0.01$). The unoperated control data were not analysed because of the reduced sample size. But, the normative data from Experiment II, Chapter 5, can be taken as an indication of the behaviour pattern observed with the unoperated animals.

The mean pre/post-operative (ppo) S.E.R.I. scores are shown in Table 9B for the same subjects as in Experiment I, Wellington and Plugg. For Wellington (Figure 6.4A) an ANOVA indicated a significant ppo X condition interaction effect, $F(5,15)=5.5$, $p<0.01$. Further analysis of the pre-operative data showed a significant condition effect where $F(5,15)=13.44$ and $p<0.0001$. Both the head down postures (HdEo and HdEd) produced a significantly greater behavioural response than either HoEo, HuEo, HuEu or the control objects ($p<0.01$ N-K each comparison). No significant difference was observed between the head down postures or between the remaining head postures. Post-operatively there were no significant effects of posture. But no significant ppo pair comparisons were found for any of the stimulus conditions.

Table 9A Overall effect of STS ablation on socio-emotional responses to head posture

	STIMULUS CONDITION					
SUBJECT GROUP	HoEo	HdEo	HdEd	HuEo	HuEu	C
UNOPERATED	0.83 +/-0.3	1.71 +/-0.4	1.71 +/-0.4	0.58 +/-0.2	0.25 +/-0.2	0.2 +/-0.1
STS LESION	1.77 +/-0.4	1.88 +/-0.4	1.90 +/-0.4	1.55 +/-0.4	1.80 +/-0.4	0.68 +/-0.20

Table 9B Effect of STS-lesion surgery on socio-emotional responses to head posture

	STIMULUS CONDITION					
SUBJECT GROUP	HoEo	HdEo	HdEd	HuEo	HuEu	C
UNOPERATED WELLINGTON	0.5 +/-0.3	3.1 +/-0.8	3.1 +/-0.7	0.2 +/-0.2	0.0 +/-0.0	0.2 +/-0.1
STS LESION WELLINGTON	0.7 +/-0.7	1.2 +/-0.9	1.0 +/-1.0	0.7 +/-0.7	0.7 +/-0.5	0.1 +/-0.1
UNOPERATED PLUGG	1.5 +/-0.6	1.7 +/-0.2	1.2 +/-0.5	1.2 +/-0.2	0.5 +/-0.5	0.0 +/-0.00
STS LESION PLUGG	0.0 +/-0.1	0.0 +/-0.1	0.0 +/-0.1	0.2 +/-0.2	0.0 +/-0.0	0.05 +/-0.05

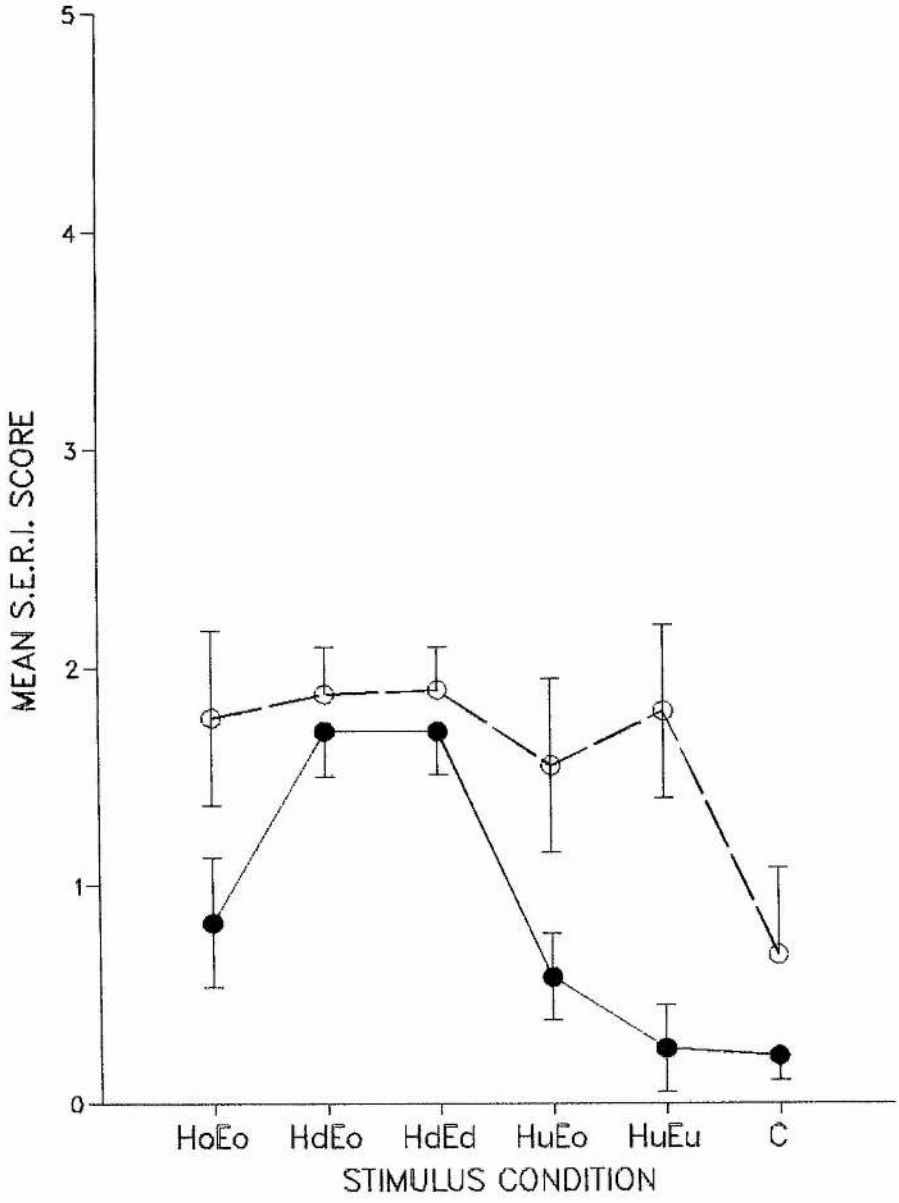


Figure 6.3 Overall effect of STS ablation on sensitivity to head posture. Socio-emotional response index (S.E.R.I.) scores indicated the inability of the STS-lesioned animals (but not the unoperated animals) to discriminate between the head down posture and other head orientations. H, head angle; E, eye angle; o, level with viewer; d, down 45 degrees from o; u, up 45 degrees from o; C, non-face controls. Filled circle/solid line, unoperated group; open circle/dashed line, STS-lesioned group. (Non-overlapping error bars only are shown.)

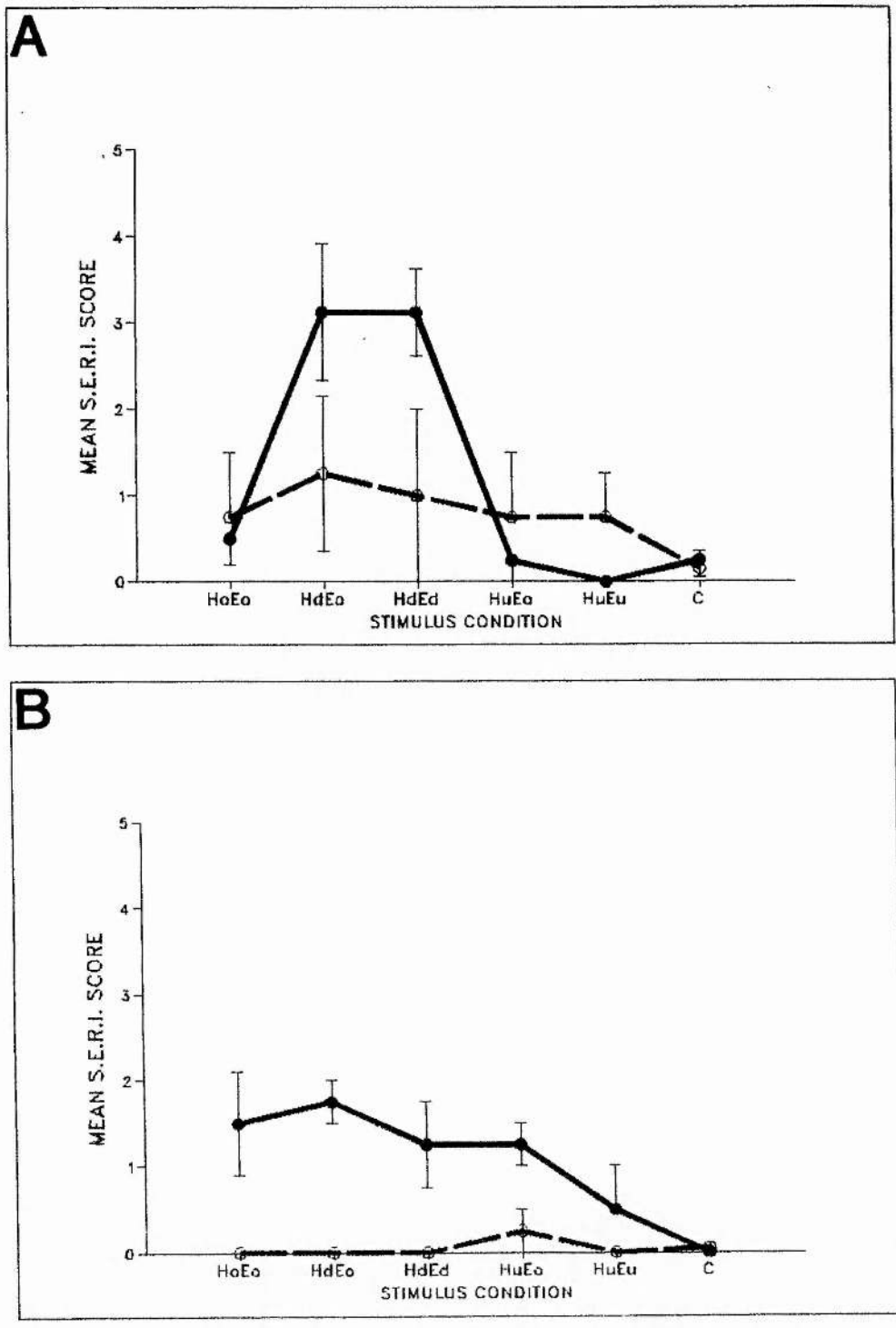


Figure 6.4 Effect of STS ablation surgery on sensitivity to head posture in two monkeys. Comparison of pre- and post-operative performance (measured by the S.E.R.I.) for both Wellington (A) and Plugg (B) indicates a reduced sensitivity to the head down (Hd) postures post-operatively. Filled circle/solid line, pre-operative; open circle/dashed line, post-operative. (Non-overlapping error bars only are shown.)

For Plugg (Figure 6.4B) an ANOVA also revealed a significant ppo X condition interaction, $F(5,15)=4.32$, $p<0.05$. For the pre-operative data further analysis showed a condition effect significant with $F(5,15)=3.21$ and $p<0.05$. One head down posture alone, HdEo, elicited a significantly greater response than the control objects ($p<0.05$ N-K); no other significant differences were found. The post-operative data demonstrated no condition effect, i.e. no discriminations between stimuli were made post-operatively. Pre/post-operative pair comparisons indicated significant differences for the HdEo and HuEo postures only ($p<0.01$ and $p<0.0001$ respectively).

In summary, the analysis of the overall pattern of responsivity to head postures revealed that STS-lesioned animals tended not to discriminate between head postures considered to have differing social value. This was in contrast to the unoperated animals' behaviour recorded in the previous chapter.

6.4 Discussion

It was suggested that the superior temporal sulcus (STS) might be the area of neocortex providing specific visual input to subcortical structures of the monkey brain organizing affective responses. An interruption in this system could be reflected in a difficulty in discriminating between socially relevant stimuli and responding appropriately to them. This hypothesis was supported by the observations and findings from both experiments.

The STS lesion caused a disruption in two ways: (1) whereas unoperated animals showed an increased responsiveness to normal face configuration, STS-lesioned animals did not; and (2) again in contrast to the unoperated animals, the STS-lesioned appeared unable to discriminate between head postures (and eye gaze) defined previously as either threatening or non-threatening. This change in affective behaviour was not coupled with a visual pattern discrimination deficit as the monkeys in this lesion group appeared well able to discriminate between the test stimuli (primate face, and head and torso models) and the control stimuli (complex 3-dimensional non-face objects).

Further evidence for this selective visual performance impairment was shown by Heywood and Cowey (1987) who tested the same subject monkeys on a battery of visual discrimination tasks. They found no significant impairments for any of the STS group (compared with unoperated control animals) on any of the tasks, which included pattern discrimination - cross versus square and horizontal versus vertical gratings; colour discrimination - black versus white and red versus green; and face discrimination - four black and white photograph pairs (two rhesus, two cynomolgus) comparisons. They did, however, show some impairment on a task requiring discrimination between directions of eye gaze, eye contact and eye aversion (Heywood and Cowey, personal communication). Their behaviour could not, therefore, be interpreted as general indiscriminate behaviour. Neither could their behaviour be explained completely as a hypoemotional state, with a general non-selective decrease in affective behaviour, since the lesioned monkeys were still capable of responding emotionally to threatening stimuli. A parsimonious

explanation would seem to be that the STS group were visually unable to differentiate socially relevant signals (face configuration, eye gaze, posture).

Except for the variety of behavioural measures scored on the socio-emotional response index (SERI) the deficits in affective behaviour of the lesioned monkeys might not have been observed. Each of the behaviours measured constitutes an element of social communicative behaviour any of which could have been subtly affected by removal of the STS. For precisely this reason the SERI was employed to reflect the STS-lesioned monkeys' performance.

In the previous experiments (Chapter 5) it was necessary only to score submissive responses to observe discriminations between the normal arrangement of facial features and jumbles, and head down threatening and non-threatening head up postures. The unoperated animals in these experiments (rhesus and cynomolgus) responded with a different repertoire of responses to those of the stumptail macaques reported in Chapter 5, although the pattern of responses was identical. The rhesus monkeys generally threatened the stimulus models whereas the stumptails lipsmacked to them. This is most probably explained as a consequence of the species on which the stimuli were based (stumptail). These variations in behavioural response between species to the same stimuli indicate in themselves the value of such a comprehensive response index.

There have been experiments which suggest that both the temporal neocortex (Myers and Swett, 1970; Horel et al, 1975) and the amygdala

(Aggleton and Passingham, 1981; Kling, 1972; Rosvold et al, 1954; Thompson et al, 1969, 1977; Thompson and Towfighi, 1976) are involved in the organization of agonistic behaviour. The emotional and behavioural symptoms associated with lesions of the temporal lobes (including the STS) and/or the amygdala signal to many observers the presence of Kluver-Bucy syndrome (Aggleton and Passingham, 1981; Bucy and Kluver, 1955; Dicks et al, 1969; Horel et al, 1975; Kling, 1972; Kluver and Bucy, 1939; Weiskrantz, 1956).

Kluver and Bucy (1939) first noted that after complete bilateral temporal lobectomy monkeys exhibited 'psychic blindness' (more commonly explained as a deficit in visual pattern discrimination), strong oral tendencies - bringing both edible and inedible objects to the mouth, hypermetamorphosia - an impulse towards action, described as excessive investigatory behaviour, profound changes in emotional behaviour, hypersexuality and changes in dietary habit (eating meat and even their own faeces). Bucy and Kluver (1955) reported typical emotional behaviour changes for one female macaque who after surgery did not lipsmack to her mirror image, approached quite fearlessly both animate and inanimate objects including snakes.

The use of the term 'fearless' here is misleading as Rosvold et al (1954) and Thompson et al (1969) have shown that animals with amygdaloid lesions exhibit context-dependent fear responses. In social situations where the lesioned animal must interact with its peers, more fear responses were observed (Thompson et al, 1969), i.e. they were 'fearful', and a postoperative fall in rank within the hierarchy was often observed (Rosvold et al, 1954). By comparison,

for lesioned animals in laboratory (non-social) situations (viewing threatening pictures of monkeys) less fear responses were noted (Thompson et al, 1969), i.e. they were more 'fearless'. Rosvold et al (1954) also found that lesioned animals in individual cages acted more aggressively.

The collection of Kluver-Bucy symptoms can be produced without the visual pattern discrimination deficit by cutting off visual inputs to the inferotemporal cortex (Mishkin, 1966); likewise many Kluver-Bucy symptoms can be produced by cutting visual inputs to the amygdala (Downer, 1961), and total amygdala destruction can produce the Kluver-Bucy symptoms again with no visual discrimination deficit (Aggleton and Passingham, 1981; Horel el al, 1975). This implies that mechanisms controlling the animal's ability to associate a visual pattern with reinforcement can be intact while mechanisms controlling behaviour are damaged (Horel et al, 1975).

To understand the visual recognition of objects it has been useful to describe two visual systems (Schneider, 1969), one for the visual location of objects and one for their identification (Mishkin et al, 1983). Perhaps to comprehend the Kluver-Bucy syndrome it might be helpful to differentiate a multiplicity of visual systems. It may be possible to disconnect the visual control from brain mechanisms organizing some of these systems while leaving in tact the control of others (Horel et al, 1975). In principle, each symptom of Kluver-Bucy syndrome could be due to disruption of a separate system each with its own visual control.

There has been little success in fractionating the Kluver-Bucy symptoms and identifying disconnection syndromes, although it has been shown that lesions to the temporal neocortex, sparing the amygdala (Horel et al, 1975; Myers and Swett, 1970; Weiskrantz, 1956) and amygdala lesions alone (Aggleton and Passingham, 1981; Dicks et al, 1969; Gloor, 1960; Goddard, 1964; Horel et al, 1975; Kling, 1972; Mishkin and Aggleton, 1981; Murray and Mishkin, 1985; Rosvold et al, 1954; Thompson and Towfighi, 1976; Thompson et al, 1969, 1977; Weiskrantz, 1956) can both produce the full Kluver-Bucy syndrome.

In an attempt to dissociate some of the abnormalities seen after total amygdalectomy Aggleton and Passingham (1981) investigated the behavioural effects of subtotal amygdaloid lesions. In contrast to the animals with total amygdaloid lesions who exhibited the typical symptoms previously described, the monkeys with subtotal amygdaloid lesions exhibited no food preference changes (they did not eat meat or faeces) - although they were more willing than control animals to investigate inanimate objects, and only minor changes in affect were observed. Extreme emotional changes were only observed in the monkey with the largest subtotal lesion. Those animals with subtotal amygdaloid lesions (that were not hypoemotional) also were not impaired on learning serial reversals of an object discrimination.

Aggleton and Passingham (1981) concluded that it was necessary to remove almost all of the visual termination regions within the amygdala to produce a disconnection syndrome. These findings are consistent with Jones and Mishkin's (1972) hypothesis that one of the functions of the amygdala may be to combine incoming sensory stimuli

with affective signals.

It is proposed here that destroying the STS cuts off cortical information, particularly that which is related to social stimuli, from the brain mechanisms (including the amygdala) that organize affect responses for agonistic behaviour. The ablation studies that tentatively reveal deficits in face perception form the major source of data for this proposal, but evidence from electrophysiological and connectional studies support this view.

Recordings of the neural activity of single cells in the STS clearly demonstrate the involvement of this area of neocortex in the analysis of biologically important stimuli, such as the face, head and body (Perrett et al, 1982, 1984, 1985a,b). Populations of neurones have been identified that respond selectively to features that play an integral role in primate social behaviour (Perrett et al, 1985b) such as eye gaze direction and head orientation. Additionally, Perrett et al (1985a) have reported cells that demonstrate a remarkable sensitivity to specific combinations of form and motion, e.g. a face moving towards the observing monkey that could characterize social gestures. One function of the STS cortex would seem to be, therefore, the visual processing of these types of ethologically relevant stimuli. Investigation of the STS's efferent and afferent connections (reviewed in Chapter 3) reveal a close association between this region of temporal cortex and the amygdala.

So, from the present study and the above reports, it appears that destruction of the STS alone can produce some symptoms of Kluver-Bucy

syndrome - a visual inability to differentiate between the social significance of certain objects and a dissociation of the stimulus from its affective qualities. This finding is only the first step in realizing the contribution that an independent area within the temporal lobe might make towards the symptoms of Kluver-Bucy syndrome. Subtotal temporal neocortex lesions in the manner of Aggleton and Passingham's (1981) subtotal amygdala lesions could increase our understanding of the system responsible for attaching or associating a percept with an appropriate emotional response.

6.5 References

Aggleton, J.P., Burton, M.J., and Passingham, R.E. (1980) Cortical and subcortical afferents to the amygdala of the rhesus monkey (Macaca mulatta). Brain Res. 190:347-368.

Aggleton, J.P., and Mishkin, M. (1983) Visual recognition impairment following medial thalamic lesions in monkeys. Neuropsychologia 21:189-197.

Aggleton, J.P., and Passingham, R.E. (1981) Syndrome produced by lesions of the amygdala in monkeys (Macaca mulatta). J. Comp. Physiol. Psychol. 95:961-977.

Bruce, C.J., Desimone, R., and Gross, C.G. (1981) Visual properties of neurones in a polysensory area in the superior temporal sulcus of the macaque. J. Neurophysiol. 46:369-384.

Bucy, C.P., and Kluver, H. (1955) An anatomical investigation of the temporal lobe in the monkey (Macaca mulatta). J. Comp. Neurol. 103:151-252.

Cowey, A., and Gross, C.G. (1970) Effects of foveal prestriate and inferotemporal lesions on visual discrimination by rhesus monkeys. Exp. Brain Res. 11:128-144.

Dicks, D., Myers, R.E., and Kling, A. (1969) Uncus and amygdala lesions: Effects on social behaviour in the free-ranging rhesus monkey. Science 165:69-71.

Downer, J.L.de C. (1961) Changes in visual gnostic functions and emotional behaviour following unilateral temporal pole damage in the split brain monkey. Nature 191:50-51.

Geschwind, N. (1965) Disconnexion syndromes in animal and man, Part 1. Brain 88:237-294.

Gloor, P. (1960) Amygdala. In: J. Field, H.W. Magoun and V.E. Hall (eds) Handbook of Physiology, Section 1: Neurophysiology, Volume II. American Physiology Society, Washington, D.C., pp.1395-1420.

Goddard, G.V. (1964) Functions of the amygdala. Psychol. Bull. 62:89-109.

Gross, C.G., Bruce, C.J., Desimone, R., Fleming, J., and Gatass, R. (1981) Cortical visual areas of the temporal lobe: Three areas in the macaque. In: C.N. Woolsey (ed.) Cortical Sensory Organization, Volume 2, Multiple Visual Areas. Humana Press, Clifton, N.J., pp.187-216.

Heywood, C.A., and Cowey, A. (1987) On the role of cortical area V4 in the discrimination of hue and pattern in the macaque monkey. J. Neurosci. 7:2601-2617.

Horel, J.A., Keating, E.G., and Misantone, L.J. (1975) Partial Kluver-Bucy syndrome produced by destroying temporal neocortex or amygdala. Brain Res. 94:347-359.

Iwai, E., and Mishkin, M. (1969) Further evidence on the locus of the visual area in the temporal lobe of the monkey. Exp. Neurol. 25:585-594.

Jones, B., and Mishkin, M. (1972) Limbic lesions and the problem of stimulus-reinforcement associations. Exp. Neurol. 36:362-377.

Jones, E.G., and Powell, T.P.S. (1970) An anatomical study of converging sensory pathways within the cerebral cortex of the monkey. Brain 93:793-820.

Kling, A. (1972) Effects of amygdalectomy on social-affective behaviour in non-human primates. In: B.E. Eleftheriou (ed.) The Neurobiology of the Amygdala. Plenum Press, New York, pp.511-536.

Kluver, H., and Bucy, P.C. (1939) Preliminary analysis of functions of the temporal lobes in monkeys. Arch. Neurol. 42:979-1000.

Mishkin, M. (1954) Visual discrimination performance following partial ablations of the temporal lobe. II. Ventral surface vs. hippocampus. J. Comp. Physiol. Psychol. 47:187-193.

Mishkin, M. (1966) Visual mechanisms beyond the striate cortex. In R.W. Russell (ed.) Frontiers in Physiological Psychology. Academic Press, New York, pp.93-119.

Mishkin, M., and Aggleton, J. (1981) Multiple functional contributions of the amygdala in the monkey. In: Y. Ben-Ari (ed.) The Amygdaloid Complex. Elsevier, Amsterdam.

Mishkin, M., Ungerleider, L.G., and Macko, K.A. (1983) Object vision and spatial vision: Two cortical pathways. Trends Neurosci. 6:414-417. Symposium No. 20. Elsevier/North-Holland Biomedical Press, pp.409-420.

Murray, E.A., and Mishkin, M. (1985) Amygdalectomy impairs crossmodal association in monkeys. Science 228:604-606.

Myers, R.E., and Swett, C. (1970) Social behaviour deficits of free-ranging monkeys after anterior temporal cortex removal. Brain Res. 18:551-556.

Perrett, D.I., Rolls, E.T., and Caan, W. (1982) Visual neurones responsive to faces in the monkey temporal cortex. Exp. Brain Res. 47:329-342.

Perrett, D.I., Smith, P.A.J., Mistlin, A.J., Chitty, A.J., Head, A.S., Potter, D.D., Broennimann, R., Milner, A.D., and Jeeves, M.A. (1985a) Visual anlysis of body movements by neurones in the temporal cortex of the macaque monkey: A preliminary report. Behav. Brain Res. 16:153-170.

Perrett, D.I., Smith, P.A.J., Potter, D.D., Mistlin, A.J., Head, A.S., Milner, A.D., and Jeeves, M.A. (1984) Neurones responsive to faces in the temporal cortex: Studies of functional organization, sensitivity to identity and relation to perception. Human Neurobiol. 3:197-208.

Perrett, D.I., Smith, P.A.J., Potter, D.D., Mistlin, A.J., Head, A.S., Milner, A.D., and Jeeves, M.A. (1985b) Visual cells in the temporal cortex sensitive to face view and gaze direction. Proc. roy. Soc. Lond. B 223:293-317.

Rosvold, E.H., Mirsky, A.E., and Pribram, K.H. (1954) Influence of amygdalectomy on social behaviour in monkeys. J. Comp. Physiol. Psychol. 47:173-178.

Schneider, G.E. (1969) Two visual systems. Science 163:895-902.

Schwartzbaum, J.S. (1965) Discrimination behaviour after amygdalectomy in monkeys: Visual and somesthetic learning and perceptual capacity. J. Comp. Physiol. Psychol. 60:314-319.

Thompson, C.I., Bergland, R.M., and Towfighi, J.I. (1977) Social and non-social behaviours of adult rhesus monkeys after amygdalectomy in infancy or adulthood. J. Comp. Physiol. Psychol. 91:533-548.

Thompson, C.I., Schwartzbaum, J.S., and Harlow, H.F. (1969) Development of social fear after amygdalectomy in infant rhesus monkeys. Physiol. Behav. 4:249-254.

Thompson, C.I., and Towfighi, J.I. (1976) Social behaviour of juvenile rhesus monkeys after amygdalectomy in infancy. Physiol. Behav. 17:831-836.

Weiskrantz, L. (1956) Behavioural changes associated with ablation of the amygdaloid complex in monkeys. J. Comp. Physiol. Psychol. 49:381-391.

Weiskrantz, L. (1970) Visual memory and the temporal lobe of the the monkey. In: R.E. Whalen, R.F. Thompson, M. Verzeano, and N.M. Weinberger (eds) The Neural Control of Behaviour. Academic Press, New York, pp.239-256.

CHAPTER 7

Neurophysiological investigations of the visual properties of cells selective for facial expression and whole body posture: Non-verbal signals in social communication.

7.1 Introduction

Interest has grown steadily in the expressive movements and postures of animals since Darwin's (1965, first published in 1872) popular account of 'The Expression of the Emotions in Man and Animals'. Since this superficial interpretation of expressive movements, accounts of primate behavioural repertoires have looked towards the motivation and consequences of displays acting as social releasers; that is, expressive movements have been considered in terms of their social communicative function (Bertrand, 1969; Chalmers, 1979; Chance, 1962; Hinde and Rowell, 1962; Marriott and Selzen, 1978; Steklis and Raleigh, 1979; van Hooff, 1962).

Non-verbal communication signals include gestures, head movements and other bodily movements, posture, facial expression and direction of eye gaze (Argyle, 1975). The importance of facial expressions, in particular, in primate social communication has been highlighted by the evolutionary trend towards increased facial mobility in primates (Andrew, 1963) brought about by the high degree of specialization undergone by the muscles in the facial region. In macaque monkeys the

facial region is also relatively devoid of hair which Kingdon (1980) believes is related to improving the visibility of facial expressions. The posture of the body, although perhaps not as powerful an effector in social interactions as facial expression, can convey specific information about an animal's rank and mood (Bertrand, 1969; Hinde and Rowell, 1962).

Animals conduct their entire social life by means of non-verbal communication in order to form alliances, find mates, rear infants, cooperate in groups, establish dominance hierarchies, interact with predators and so on (Argyle, 1975). As there is no doubt that communication by expressions and postures (non-verbal signals) is of primary importance to socially organized monkeys it is easy to speculate the existence of neural mechanisms evolved to produce (e.g. Darwin, 1965) and comprehend facial expressions.

In effect a large area of the cortex of the brain is devoted to both motor and somatosensory representations of the face (Penfield and Rasmussen, 1950) and visual representations of the face have been identified across a number of brain regions, i.e. face-sensitive cells have been reported in frontal cortex (Pigarev et al, 1979), parietal cortex (Leinonen and Nyman, 1979), the amygdaloid cortex (Leonard et al, 1985; Rolls, 1981) and profusely in the temporal cortex (e.g. Baylis et al, 1985; Bruce et al, 1981; Gross et al, 1972; Leonard et al, 1985; Perrett et al, 1982, 1984, 1985b). Although the voluntary control of communicative abilities is assumed as a role of the cortex (Steklis and Raleigh, 1979) as yet no veridical visual representation of facial expression (just one

communicative element) is known.

Neurophysiological and behavioural evidence have suggested that the polysensory cortex of the superior temporal sulcus (STS) functions to regulate social behaviour (Leonard et al, 1985; Perrett et al, 1982, 1984, 1985b) by providing a visual analysis of socially relevant stimuli. It is well documented that face-sensitive cells have been recorded in this region of the cortex (Bruce et al, 1981; Baylis et al, 1985; Desimone et al, 1984; Gross et al, 1972; Leonard et al, 1985; Perrett et al, 1982, 1984, 1985b, 1987b; Rolls, 1981) as well as cells sensitive to the presence and form of the body (e.g. Perrett et al, 1985a, 1987a).

In addition, cells in the STS have been observed selectively responsive to direction of eye gaze, a cue central to the interpretation of expression; and a few cells have been reported sensitive to degree of mouth opening, although their potential involvement in expression analysis has not been systematically studied. It would appear then from such evidence that the STS could be the site of a representation of communicative elements concerning the head and body. Adding weight to this argument, ablation studies of the STS have revealed impairments in discrimination of socially relevant stimuli including head posture and eye gaze (Chapter 6; Cowey and Heywood, unpublished studies).

The present study was therefore concerned with investigating the properties of face and body-sensitive cells in the STS to determine whether they exhibited any selectivity for the expression of the face

or the posture of the head or body (previously unexamined non-verbal signals), and on what visual features of the stimulus any observed sensitivity was based. Sensitivity to the neutral face and a variety of threatening and appeasing expressions was explored along with the independent or associated cue of vertical head orientation (cf Chapter 4) as certain expressions may be unambiguously characterized by a particular head orientation (Bertrand, 1969; Hinde and Rowell, 1962; van Hooff, 1962).

Similarly, the orientation of the head may be defined with respect to the body, the posture of which may independently signify an animal's rank in a dominance hierarchy and its emotional status. So, cellular sensitivity to the posture of the body was explored by comparing body-sensitive cells' responses to postures adopted by the monkey in different forms of behaviour, namely: A sitting or crouched posture utilized as a resting position or by a subordinate after attack; a bipedal posture used in feeding or to locate or carry objects; and a quadrupedal posture most commonly adopted in walking or threat situations (Bertrand, 1969; Hinde and Rowell, 1962; van Hooff, 1962).

Cells in the STS were found sensitive to the sight of these non-verbal communicative signals (preliminary report, Perrett et al, 1985b) responding either to individual features of the expressive face or body or to a combination of these features that characterized the expression or posture. The evidence for and the suitability of the STS as a neural mechanism underlying social communication in the monkey is discussed.

7.2 General Methods

To investigate the properties of cells demonstrating visual selectivity the standard techniques (described in Chapter 2) for single unit recording in conscious, behaving monkeys were employed. The common methodological approach is described for experiments investigating both the selectivity of face-sensitive cells for facial expression and the selectivity of cells, sensitive to the head and body, for posture - i.e. the orientation of one body part with respect to another. The procedure for examining the cells' responses, the testing protocol for cells sensitive to visual stimuli, and the type of stimuli employed are outlined below.

7.2.1 Subjects

Two rhesus macaques (Macaca mulatta), Perry (P) and Fiona (F), previously trained on a visual discrimination task (2.3), provided visual data for Experiments I and II over a total period of three years. The general recording procedure is described in 2.6.

7.2.2 Stimuli

(a) Face stimuli

Face stimuli included the faces of the experimenters, doll faces, colour slides, photographs and videotapes of human and monkey faces.

Real faces were presented to the monkey oriented in different directions and with different expressions. For each pose the orientation of the face was characterized by the angle the stimulus face made with the line of sight of the monkey. In the horizontal plane poses included full face, left or right profile and back of the head (0, 90 and 180 degrees respectively); in the vertical plane other poses included head up (head pointing up 45 degrees to the axis of the torso) and head down (head pointing down 45 degrees to the axis of the torso). Head orientation is illustrated in Figure 7.1.

Non-human primate facial expressions were mimicked by the experimenters so that a stimulus array of real face expressions included neutral face, aggressive threat face, yawn, grin and grimace (or silent bared teeth threat face). Dynamic gestures included lip-smacking, teeth-chattering and chewing (of food). These are illustrated in Figure 7.2.

The compound facial expressions were characterized by their component features from Bertrand (1969), Hinde and Rowell (1962) and van Hooff (1962): Neutral face - facial elements in their "neutral" position; aggressive threat face - direct eye gaze at partner, raised eyebrows, ears flattened against the head, mouth slightly or fully open but teeth not visible; yawn - head thrown backwards, mouth open wide with canine teeth often visible; grin - eye gaze contact with partner or head turned away, mouth more or less closed but lips retracted and mouth-corners pulled back baring teeth; and grimace - similar to the grin but the mouth may be slightly opened.

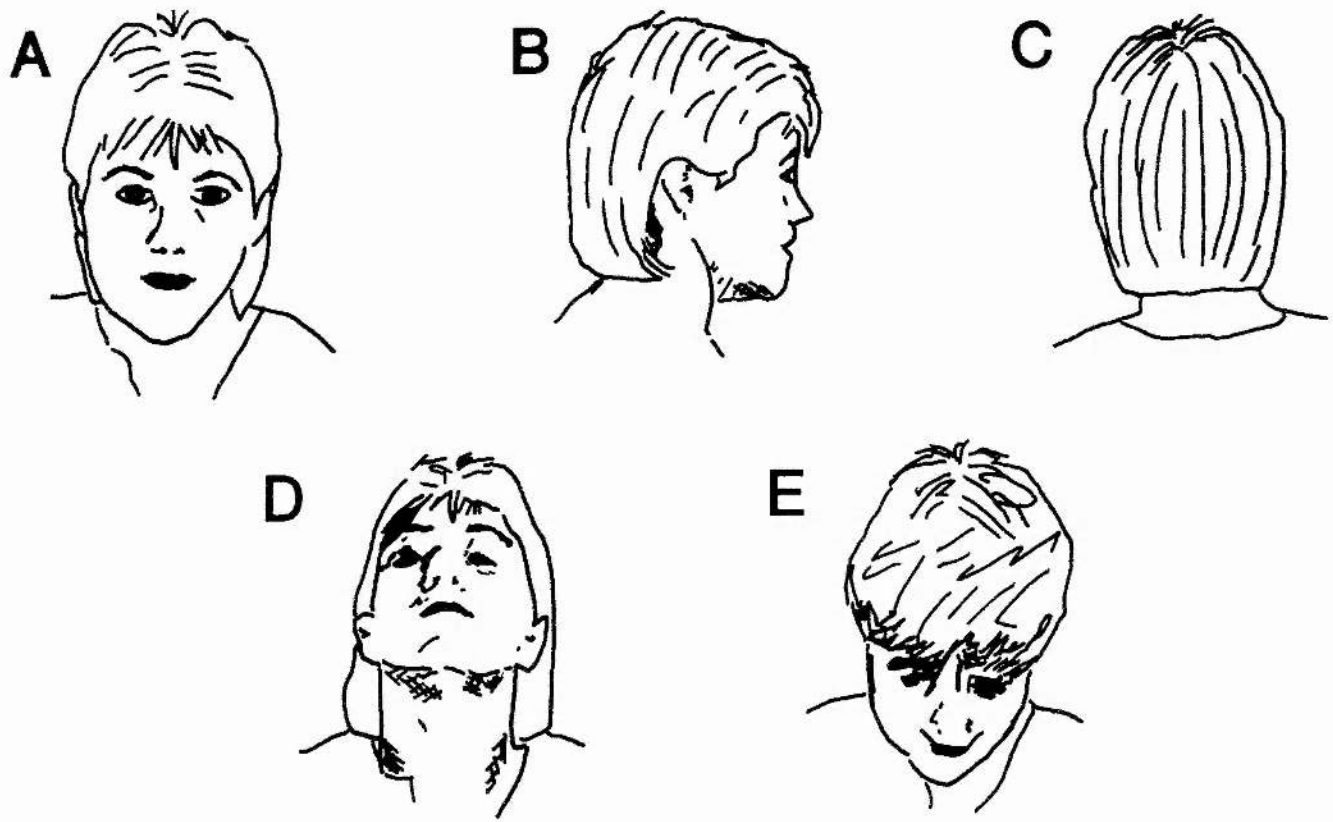


Figure 7.1 Schematic representation of stimulus examples of human head orientation. A, full face (0 degrees); B, profile face (90 degrees); C, back of head (180 degrees); D, full face head up (Hu); E, full face head down (Hd). All faces are depicted with a neutral facial expression.

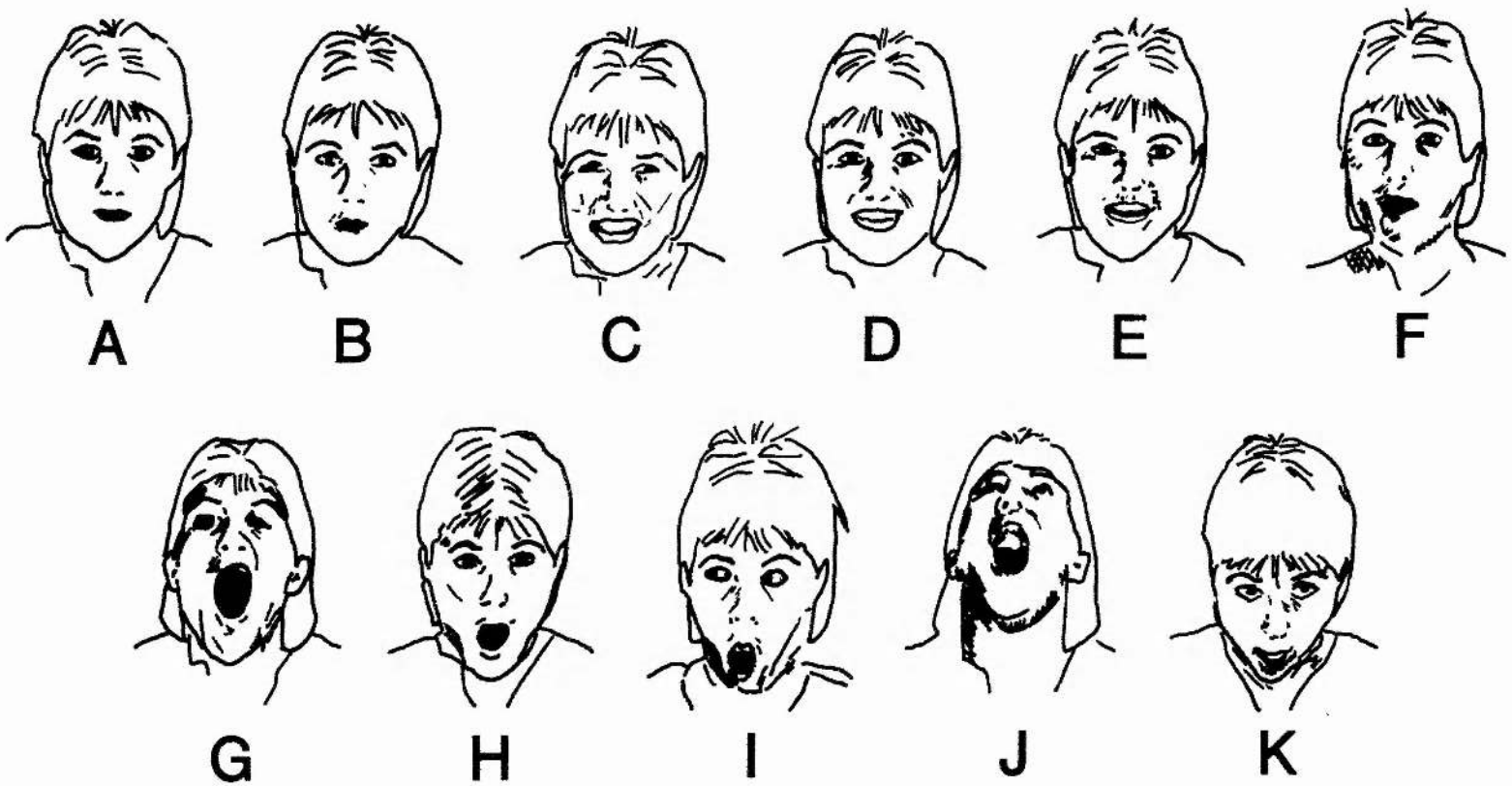


Figure 7.2 Stimulus set of monkey facial expressions imitated by a human experimenter. A, neutral; B, lipsmack; C, teethchatter; D, grin; E, grimace; F, chew; G, yawn; H, threat; I, threat with eyes averted; J, head up open mouth expression; K, head down open mouth expression. All expressions are depicted in full face.

In lip-smacking, the eyes stare at the partner, the ears are retracted, the mouth-corners are pulled back and the mouth and lips simultaneously open and almost close, rapidly. The teeth-chattering face is closely related to the lip-smacking face being likewise characterized by a rapid opening and closing of the mouth. Here, however, the lips are fully vertically retracted thus baring all the teeth which meet when the mouth is closed (van Hooff, 1962).

A videotape of macaque monkeys with these expressions and gestures was also prepared so that identical stimuli could be presented to the viewing monkey for different cells. For the 'expression' tape, edited from free playing film of macaque monkeys demonstrating the gamut of threatening and appeasing expressions, a one second blank film preceded and followed a one second film of each expression. (Only the head of the monkey was visible to the viewer and all expressions were performed directly to the camera and hence the viewer.) These facial expressions are illustrated in Figure 7.10. Photographs and slides of human and monkey face views and monkey expressions were also available as stimuli.

Human faces were primarily used to examine the importance of individual facial elements in face and expression sensitivity as parts or regions of the face were independently easy to manipulate. In this way the contribution of the mobile features of the face in particular (namely the eyes and the mouth) could be assessed. Alternatively, and in addition, areas of the face were presented in isolation by occluding the remaining features with a piece of blank card.

(b) Posture stimuli

Stimuli used to understand cells' sensitivity to posture included the bodies of experimenters, a full-sized model stumptail monkey (see 5.2.2) and photographs and colour slides of monkey postures. The head and body of an experimenter (or the three-dimensional model monkey) were presented to the subject monkey in one of three body postures characterized as: Bipedal - head and torso and limbs held vertically; quadrupedal - torso and head horizontal with the body supported on four limbs; and crouch - head vertical with the torso bent low and the limbs pulled up together. These are illustrated in Figure 7.3. Videotape of a colony of macaque monkeys adopting a variety of postures was also available as a stimulus. Individual sequences of film illustrating movements from one posture to another were identified and utilized as repeatable stimuli.

The visual basis of the cells' postural sensitivity was examined in the same manner as for the expression-sensitive cells. To distinguish the important features of the stimulus, independent regions of the whole body were manipulated to present, for example, a quadrupedal body with an upright head or a bipedal body with head oriented down (rather than the more obvious head down and head up orientations respectively). Alternatively, regions of the whole body were occluded by a black screen or a heavy black curtain so that specific areas of the body such as the head alone, the body alone, or the upper half of the body were presented in isolation as stimuli.

(c) Other stimuli

A large number of three-dimensional objects were collected, differing

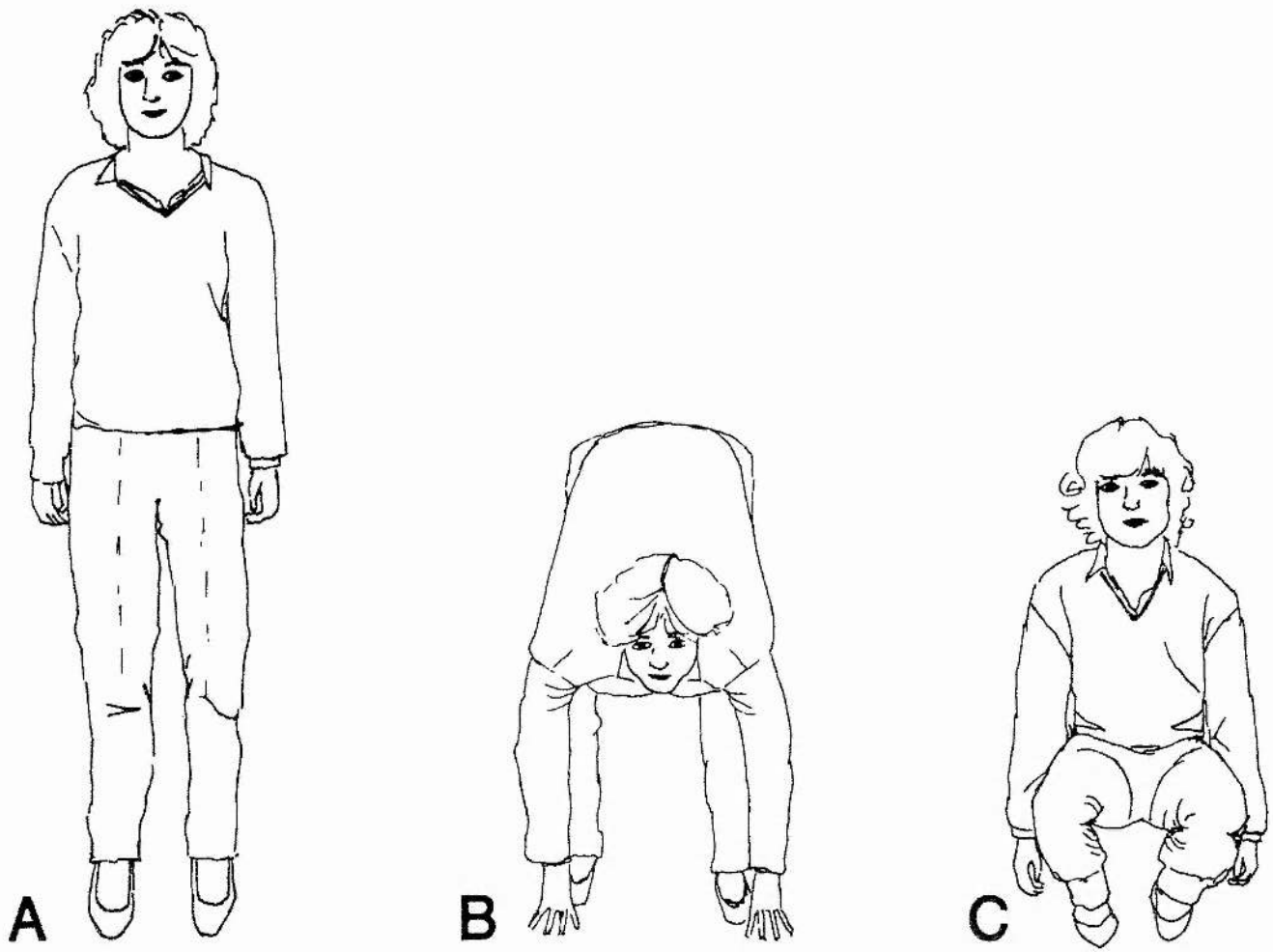


Figure 7.3 Stimulus set of monkey body postures characterized by a human experimenter. A, bipedal stance; B, quadrupedal stance; C, crouch. Full face views only are shown.

from one another in size, shape, colour, surface pattern and texture. The objects ranged in size from 10cm in length to objects the size of a person, so that they could act as appropriate controls in both the face and posture experiments. Two-dimensional stimuli included photographs of black and white, vertical or horizontal gratings varying in contrast and spatial frequency, simple geometrical patterns and complex patterns found in magazines etc, mounted on card.

7.2.3 Stimulus presentation and testing protocol

Visual stimuli were presented from behind a large aperture shutter (Compur Electronic 5FM 6.4cm aperture), secured in front of the subject monkey's face, after a 0.5s signal tone of 700Hz. The duration of the shutter opening, i.e. stimulus presentation time, was 1s. All the stimuli were presented against uniform backgrounds, either a large white back board or a black material screen.

Real stimuli and photographic stimuli were presented to the monkey approximately 0.3-1m from the monkey's face and slides back projected onto a white screen 1-3m from the monkey. The prerecorded videotape films were replayed to the monkey in minimal room lighting on a 26" television screen (Barco DCD 2740 F) placed central to the monkey, 1-3m from its face. An entire film sequence was played through to the monkey for clinical testing or the one second edited film sequences (or 'freeze-frame' images from the screen) were timelocked for presentation with the opening of the monkey's viewing shutter.

The testing protocol for each cell was similar to that described for visual stimuli in 4.2.3. Responses to all stimuli were compared to determine if the cell demonstrated any selectivity. (If a cell's signal to noise ratio exceeded 2:1 on presentation of any visual stimulus, that cell was classified as a visual cell.) If cells showed a selectivity for faces or head and body posture (i.e. responded at a consistently high firing rate to these but not other stimuli) the specific testing for sensitivity to face view, facial features and head and body orientations could be performed by presenting the stimuli described.

Stimuli were presented in a pseudorandom order with no fixed interstimulus interval. The number of stimulus trials given to the monkey, for each cell, was dependent on the length of time it was actually possible to record from that cell and the quality of the signal. Where possible an attempt was made to equalize the numbers of trials of a stimulus for each cell. (Data were collated and analyzed as explained in Chapter 2.)

7.3 Results

Only those cells that responded visually to the sight of faces or other views of the head and body and particularly to face expression and head and body postures are considered here. A detailed account of other properties of these visual cells encountered in the same brain area is given in Perrett et al (1984, 1985a,b). A total of 244 tracks

in two monkeys were directed to traverse the upper and lower banks and fundus of the STS. A total population of 2780 cells was isolated and studied in these monkeys, but only a small population of these cells is described here. In Perry (P) 92 cells (of 1227 cells recorded in the STS, 7.5%) responded selectively to faces and bodies presented to the subject monkey. In Fiona (F) extensive sampling of somatosensory cells (Chapter 4) resulted in limited sampling being conducted in the "face" area of the anterior STS (see 7.3.1), so a smaller population of cells (29 out of 1553 cells in the STS, 1.9%) were encountered selective for faces and bodies here.

7.3.1 Histology

Recordings were made in the right hemisphere of the monkey, Fiona, at the same anterior-posterior coordinates as described previously in the tactile study (Chapter 4).

Although the majority of neurones sensitive to visual aspects of the face and body were located in the same regions of the anterior, upper bank of the STS cortex as the tactile-sensitive cells (4.3.1, Figure 4.1), they were generally found to be more medial to these cells. This is illustrated in Figure 7.4.

For a second monkey, Perry, cells in the STS were extensively examined in the left hemisphere, where a high concentration of head and body-sensitive cells were found. A reconstruction of the position of the head-sensitive cells is given in Figure 7.5. As for Fiona, this

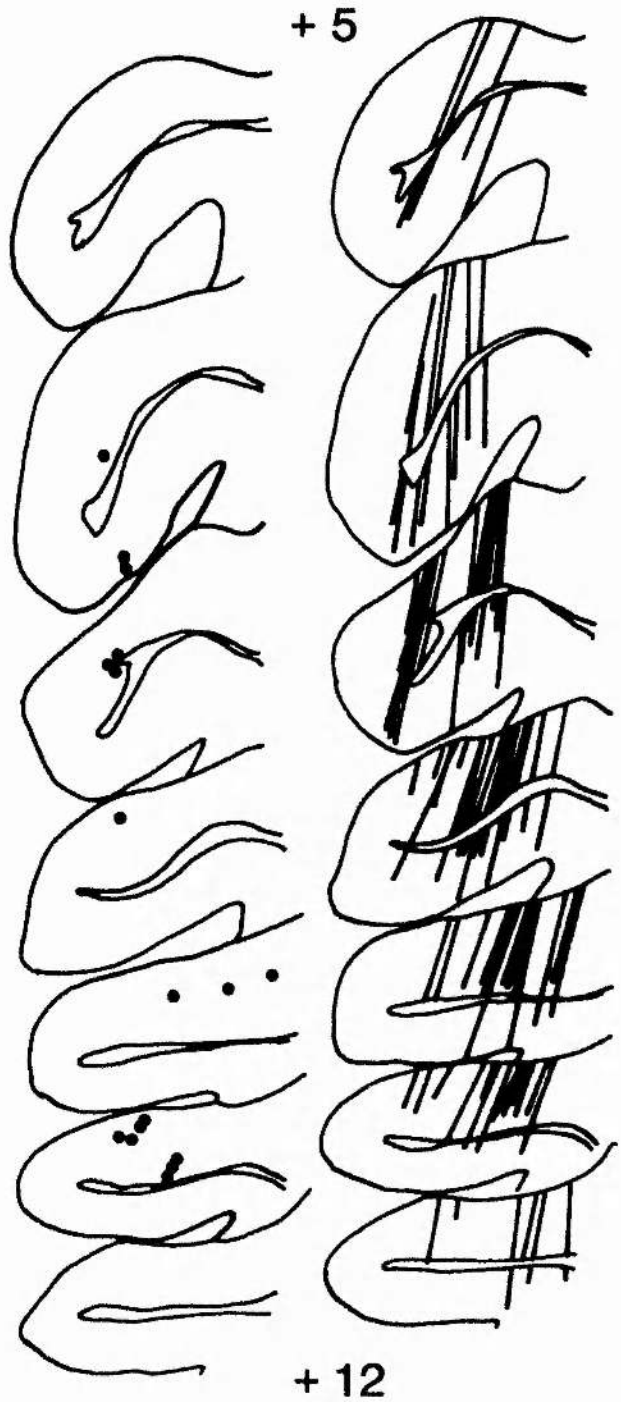


Figure 7.4 Distribution of face-sensitive cells in the temporal cortex (right hemisphere) of monkey, Fiona. Enlargement of the superior temporal sulcus (shown in coronal sections from +5 to +12mm anterior of the interaural plane) showing (right) the position of cell recording tracks; and (left) the medial location of cells responsive to any view or expression of the face (head).

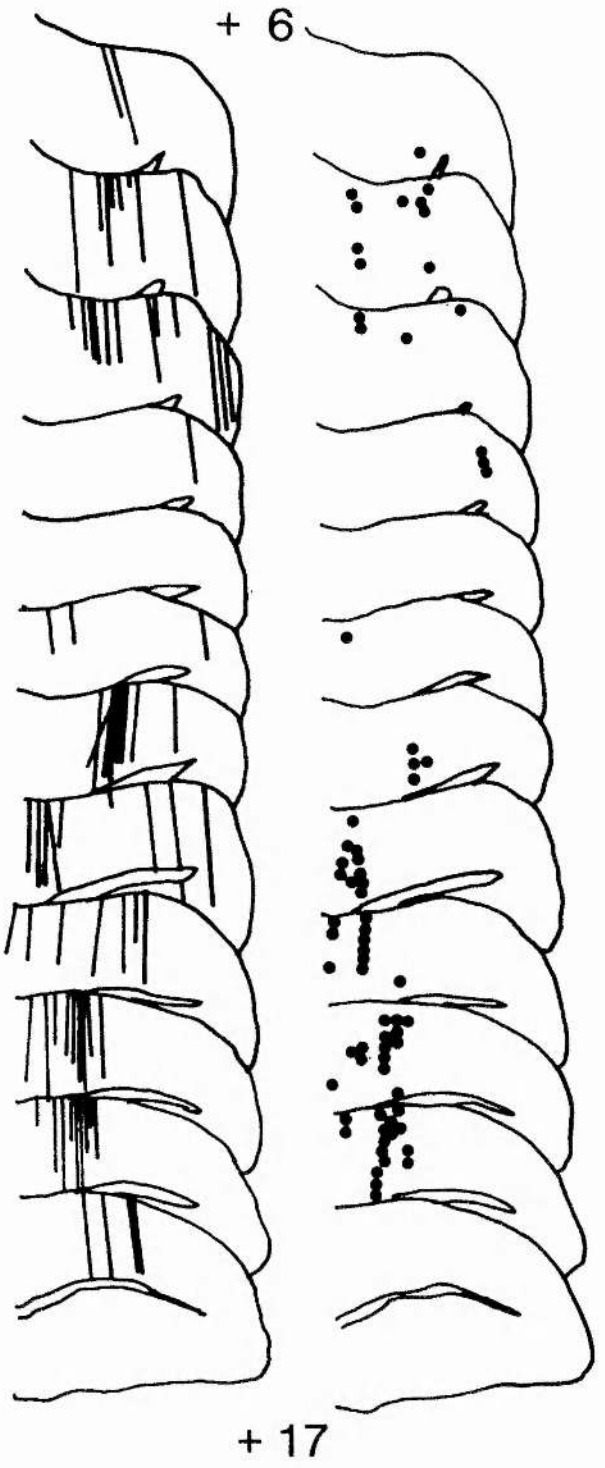


Figure 7.5 Distribution of head and body-sensitive cells within the temporal cortex (left hemisphere) of monkey, Perry. Enlargement of the superior temporal sulcus (shown in coronal sections from +6 to +17mm anterior of the interaural plane) showing (left) position of cell recording tracks, and (right) the location of cells responsive to any view of the face or head.

type of cell is located medially, in a separate location from the touch-sensitive cells, and other classes of visual cells (Perrett et al, 1984, 1985a, 1987a).

7.3.2 General cell characteristics

Cells in the STS responsive to expression and posture were unresponsive to a variety of simple and complex non-face objects such as bars, gratings, toys e.g. patterned ball, and food objects e.g. banana. This specificity exhibited by all the neurones described in this chapter is illustrated in Figure 7.6 for an expression-sensitive cell (F108). Here, each facial expression elicited a significantly greater response ($p<0.01$ Newman-Keuls, each comparison) than the non-face objects classified together as control stimuli. Cell activity in response to the control stimuli did not differ significantly from the cell's spontaneous activity (s.a.). For all the cells described images of a stimulus were sufficient to activate the cell. Dynamic images generally elicited equivalent responses, i.e. motion was not observed to enhance the cells' responses in this study.

All cells had non-habituating excitatory responses to the head and body stimuli that were precisely time-locked to the presentation and duration of the stimulus (e.g. Figure 7.7). Responses were characterized by an early transient elevation to the stimulus onset followed by a gradual decay which still exceeded the cell's s.a. while the monkey fixated the stimulus (illustrated in Figure 7.8).

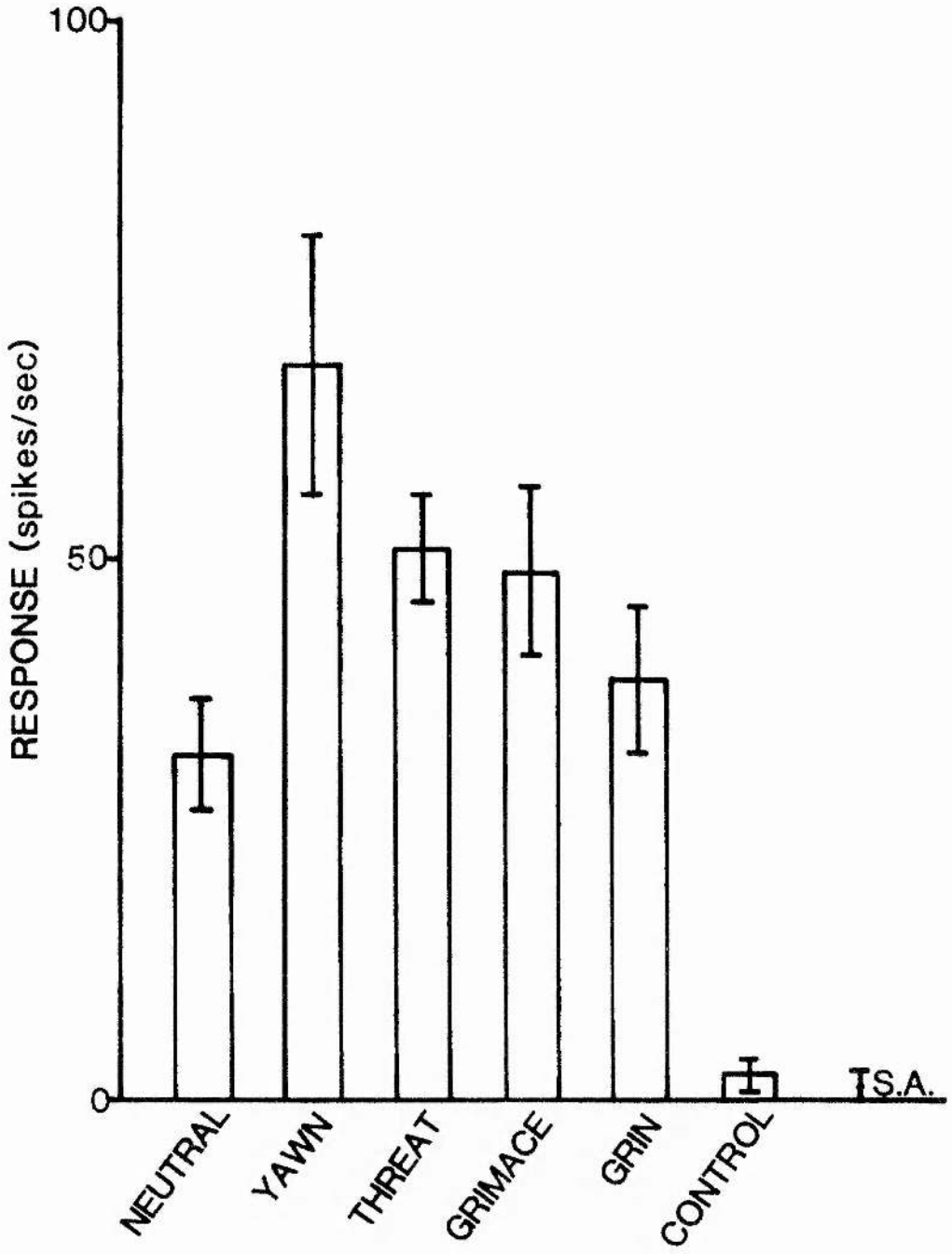


Figure 7.6 General specificity of one cell, F108, for facial expression. A neutral face gives a reduced response and non-face objects a negligible response. S.A., spontaneous activity of the cell. (Numbers of trials per condition (N)=5,2,5,3,3,5,5. Overall effect of conditions $F=23.1$, $df=6,21$, $P<0.01$.)

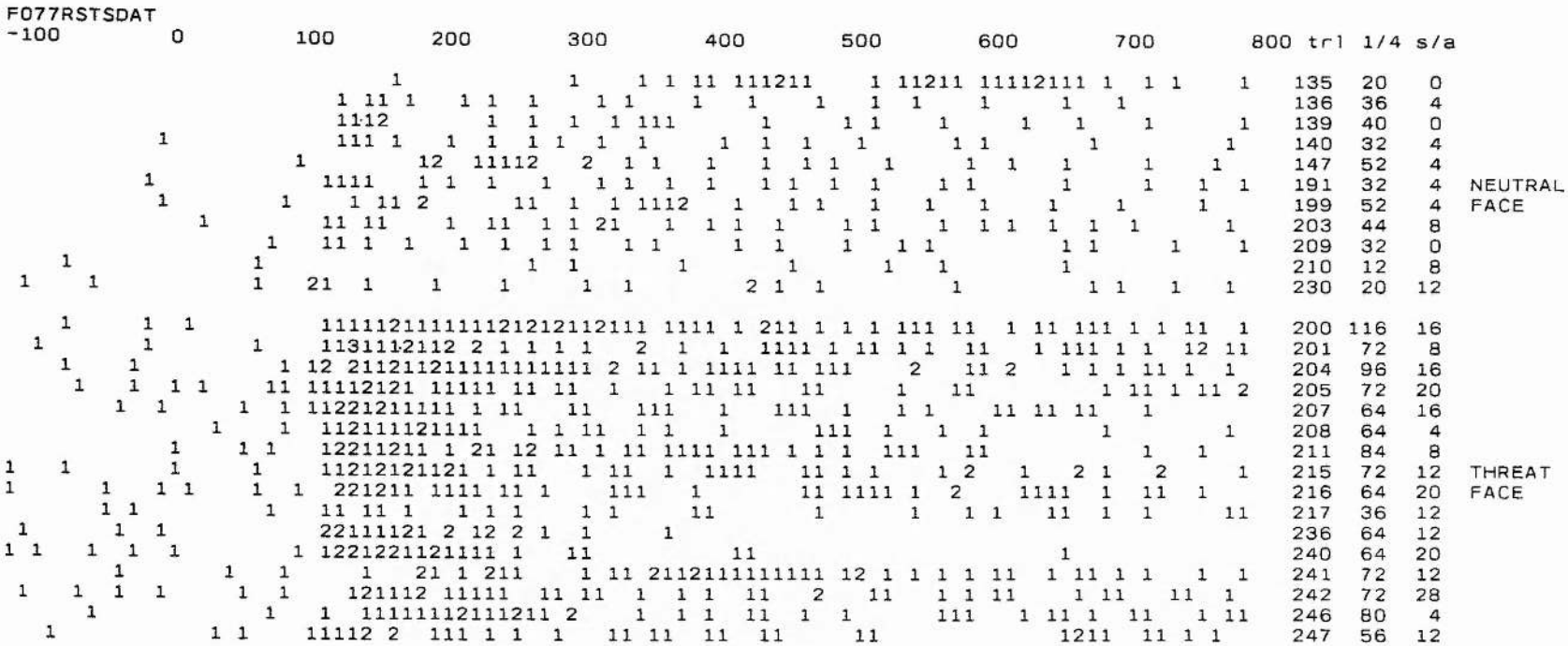


Figure 7.7 Activity of a single cell sensitive to threat facial expression. Each row reconstructs the activity of the cell during one trial showing the number of spikes occurring in successive 10ms time bins. Time relative to the opening of a shutter and presentation of stimuli is given at the top of the figure. Eleven trials for presentation of a face with neutral expression and 16 trials for a threat expression are grouped together, showing the cell's increased firing rate to the threat face. The trial number (trl), cell's response (1/4, spikes/sec) and spontaneous activity (s/a) of the cell before stimulus presentation are shown to the right of the figure.

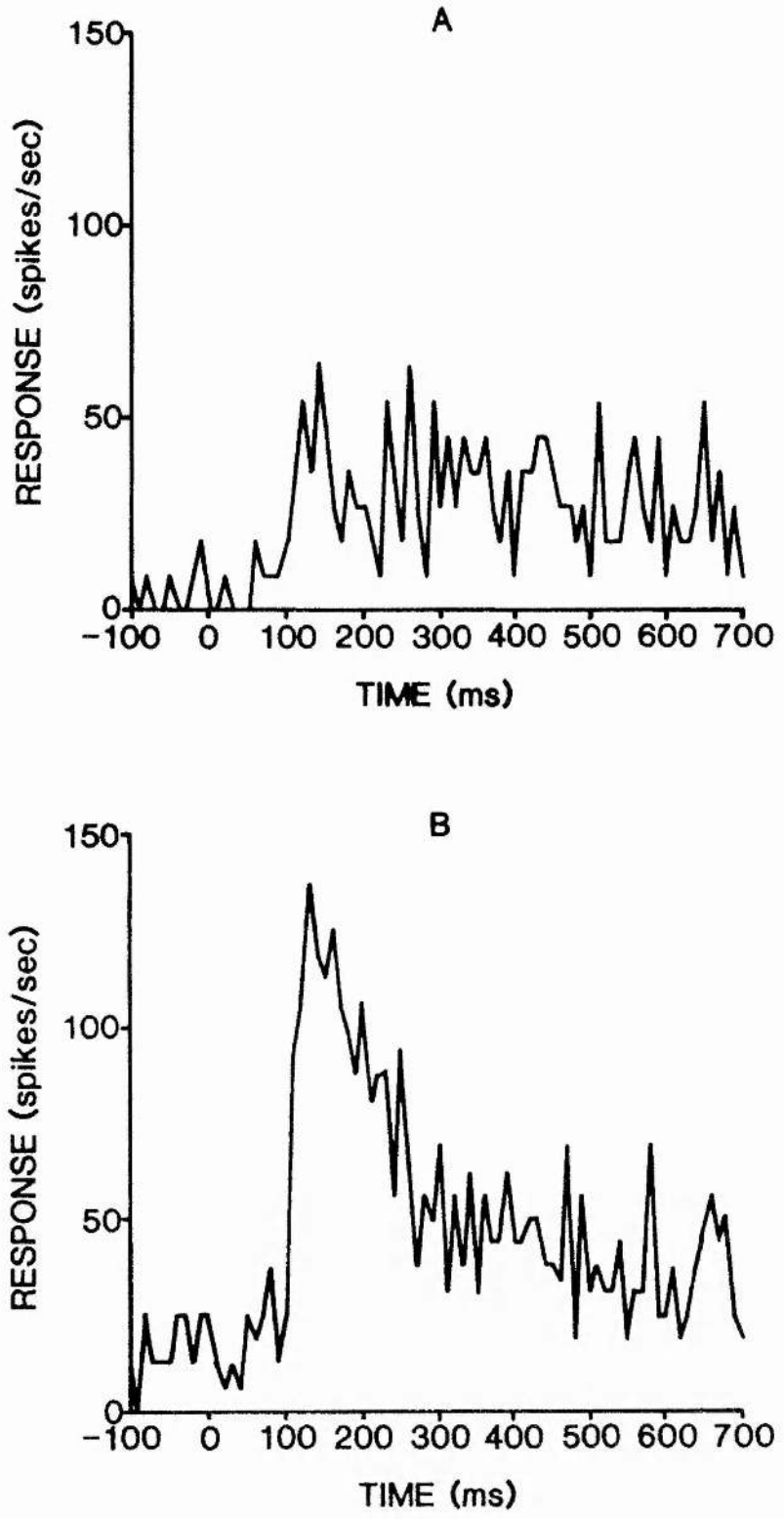


Figure 7.8 The selective response of one cell, F077A, to a threat expression illustrates the time course and latency of this visual response. The solid lines represent the average response to a human face with neutral expression (A) and a monkey's threat expression (B). The stimulus was presented at time 0ms for 1s. The spontaneous activity of the cell is indicated by pre-trial activity (-100ms to 0ms).

Such responses had visual latencies between 100 and 250ms after stimulus onset (e.g. Figure 7.8). The consistent onset latency of this type of response and the close relationship between the neural responses and the duration of the visual stimulation strongly suggested that the cells' discharges were related to the sight of the visual stimulus, i.e. they were not motor or emotional responses triggered by the stimulus. (If the neural activity had been related to some motor action, the responses observed would have been more variable in onset latency and duration.)

A variety of behaviours were exhibited in response to one stimulus, for example in response to a threat face stimulus the viewing monkey was observed to threaten back, lipsmack (appease) the stimulus and remain impassive during stimulus presentation. Regardless of the subject's behavioural actions the neural response to a stimulus remained constant, i.e. the cells did not respond as a consequence of the behaviour evoked from the viewing monkey or reflect on the monkey's emotional state.

7.3.3 Face sensitivity

Sensitivity to expression is defined here as the preferential response to one expression over another. Seven cells responsive to faces were found to give an increased response to a particular expression or expressions. Four of these seven cells showed a preference for a yawn or threat expression, two for a yawn expression and one cell for a grimace. Although the visual basis for selectivity (described later)

indicates the importance for some cells of individual facial elements in expression, these cells are referred to as expression-sensitive for ease of reference.

The cells sensitive to facial expression were generally most responsive to faces oriented directly towards the subject monkey (0 degrees). Expressions displayed after rotating the face away from the monkey horizontally toward profile (either 45 or 90 degrees) and further to the back of the head elicited reduced or no responses. For example, one expression-sensitive cell (F077a) exhibiting selectivity for face orientation (with neutral expression) in the horizontal plane is illustrated in Figure 7.9A. This cell gave a significantly larger response ($p<0.01$ Newman-Keuls each comparison) to the full face orientation (0 degrees) compared with profile and back of the head (90 and 180 degrees respectively) and the cells spontaneous activity (s.a.). The latter orientations did not differ significantly from s.a.

Four cells were specifically responsive to a threat or yawn expression responding less to neutral or appeasing expressions. This is illustrated in Figures 7.8 and 7.9B. With real human faces as stimuli (Figure 7.9B) the responses elicited by yawn and threat were significantly larger ($p<0.01$ each comparison) than that elicited by a neutral, grin or chewing face, or the cell's s.a. The grin face and chewing produced a small response significantly greater than the cell's s.a. ($p<0.05$ and $p<0.01$ respectively).

This pattern of responses to expressions of real human faces was

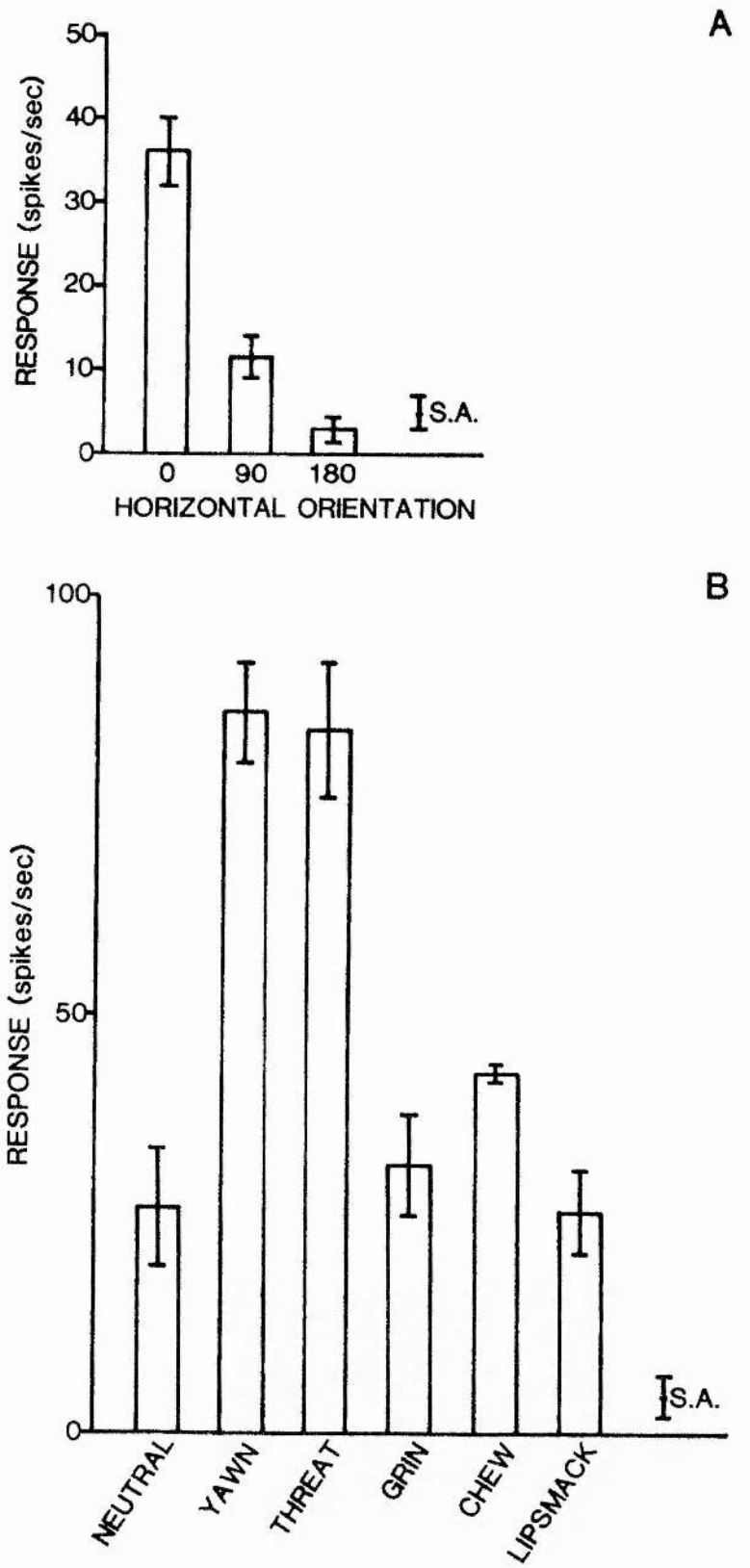


Figure 7.9 Responses of one cell, F077A, to horizontal orientation of the head and facial expression. A, the cell responds more to the full face horizontal orientation of the head (0 degrees) than to the profile face (90) or back of the head (180), (N=4, F=26.2, df=3,22, P<0.01); B, the cell also responds more to the open mouth (threat) expression than to any of the other facial expressions tested (N=5,4,5,5,5,5,5, F=22.0, df=6,22, P<0.01). S.A., spontaneous activity.

replicated using videotaped film of macaque facial expressions. Oscilloscope traces of the activity of one cell (Figure 7.10) in response to four monkey expressions - neutral, teeth-chattering , grimace and threat - indicate that the most effective stimulus for this cell (F077a) was the threat face. So, cells selectively responsive to one form of facial expression continued to respond to that expression despite changes in species (human to monkey), identity (one experimenter or monkey to another) and the stereoscopic depth of the presentation, i.e. real and three-dimensional or two-dimensional videotape).

Two cells were selective specifically for a yawn expression in which the mouth is opened vertically and also expanded horizontally to reveal the teeth. Sensitivity to this expression is illustrated for one cell, P106, (in Figure 7.11) where the response to a yawning face was greater than that to faces with open mouth threat expression, neutral expression or a fear grimace (or the cell's s.a.). Note that the presence of these cells indicated that yawn and threat could be characterized independently (see 7.4.2 for a full discussion).

Responses of a cell most sensitive to a grimace expression (F108b) are illustrated in Figure 7.12. The best response elicited by this cell was to a grimace; this differed significantly from that to an open mouth threat expression and control stimuli ($p<0.05$ each comparison), and the cell's s.a. ($p<0.01$). The responses to a yawn expression differed significantly ($p<0.05$) from the cell's s.a., but no other expressions elicited a significant response.

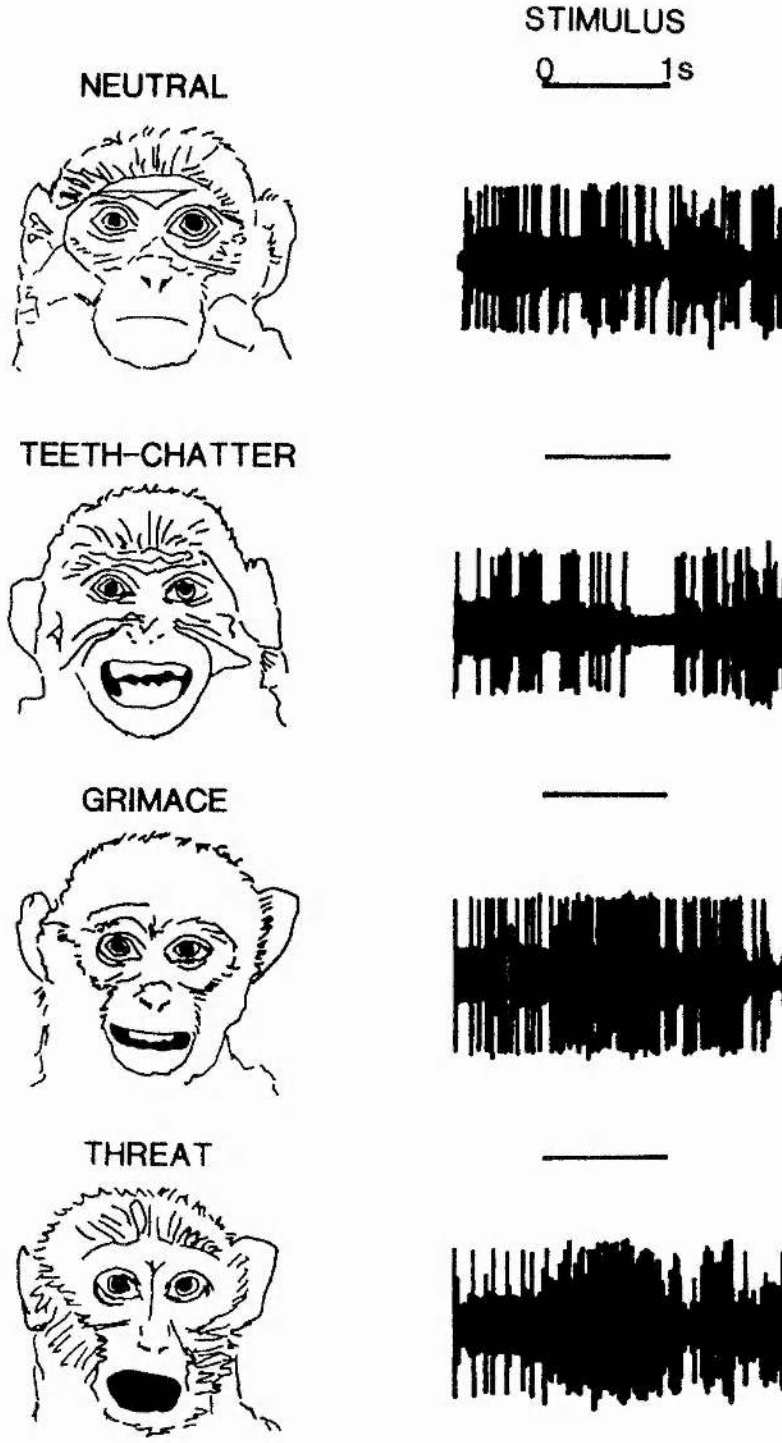


Figure 7.10 Sensitivity to threat expression. Left column illustrates a video set of different expressions of one rhesus macaque used as stimuli: Neutral; teeth-chattering (an appeasement gesture); fear grimace; open mouth threat face. Right column illustrates recordings of the spike activity of one cell, F077B, during presentation of the stimuli. The calibration bar indicates onset and duration of stimulus presentation (1s).

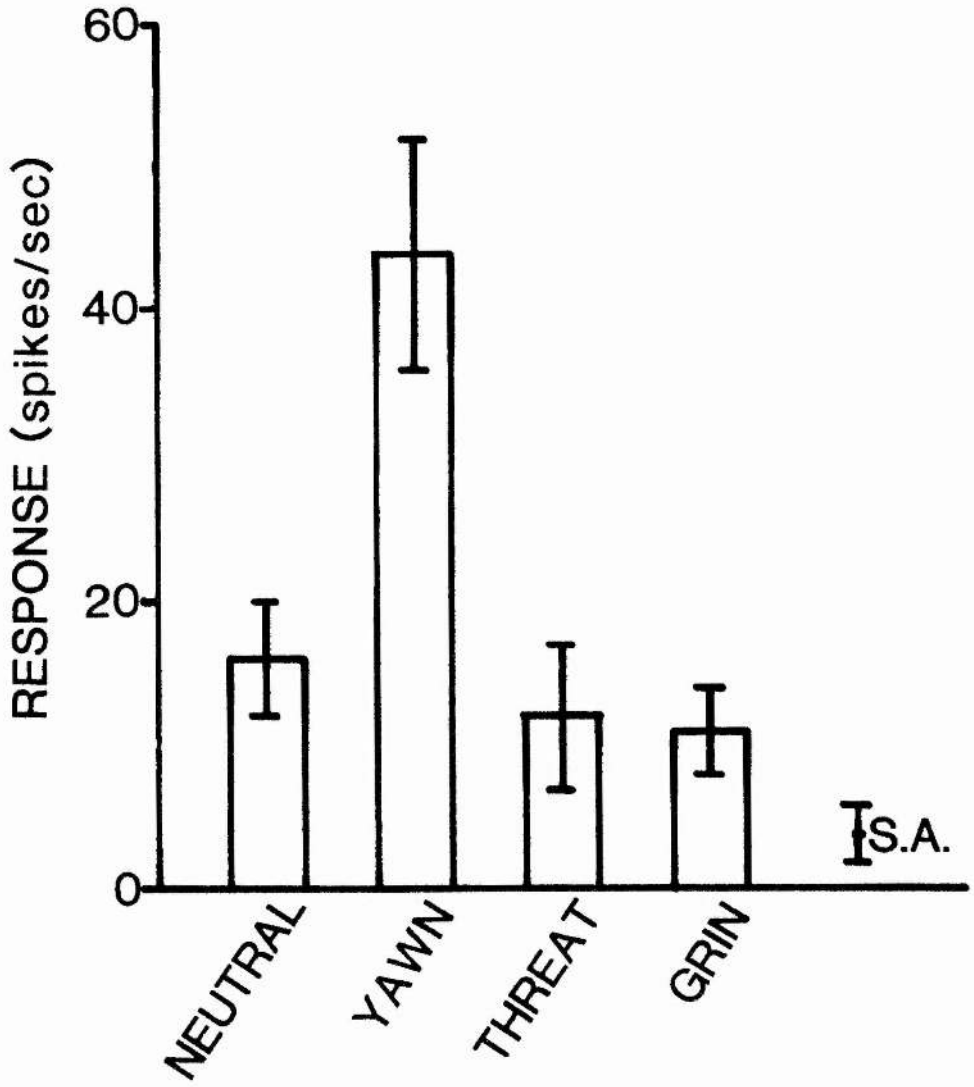


Figure 7.11 Sensitivity to a yawn facial expression. The mean and standard error of response are illustrated for cell P106. The cell responds more to a yawning face than to faces with neutral expression, open mouth threat expression or fear grimaces. S.A., spontaneous activity. (Adapted from Perrett et al, 1984.)

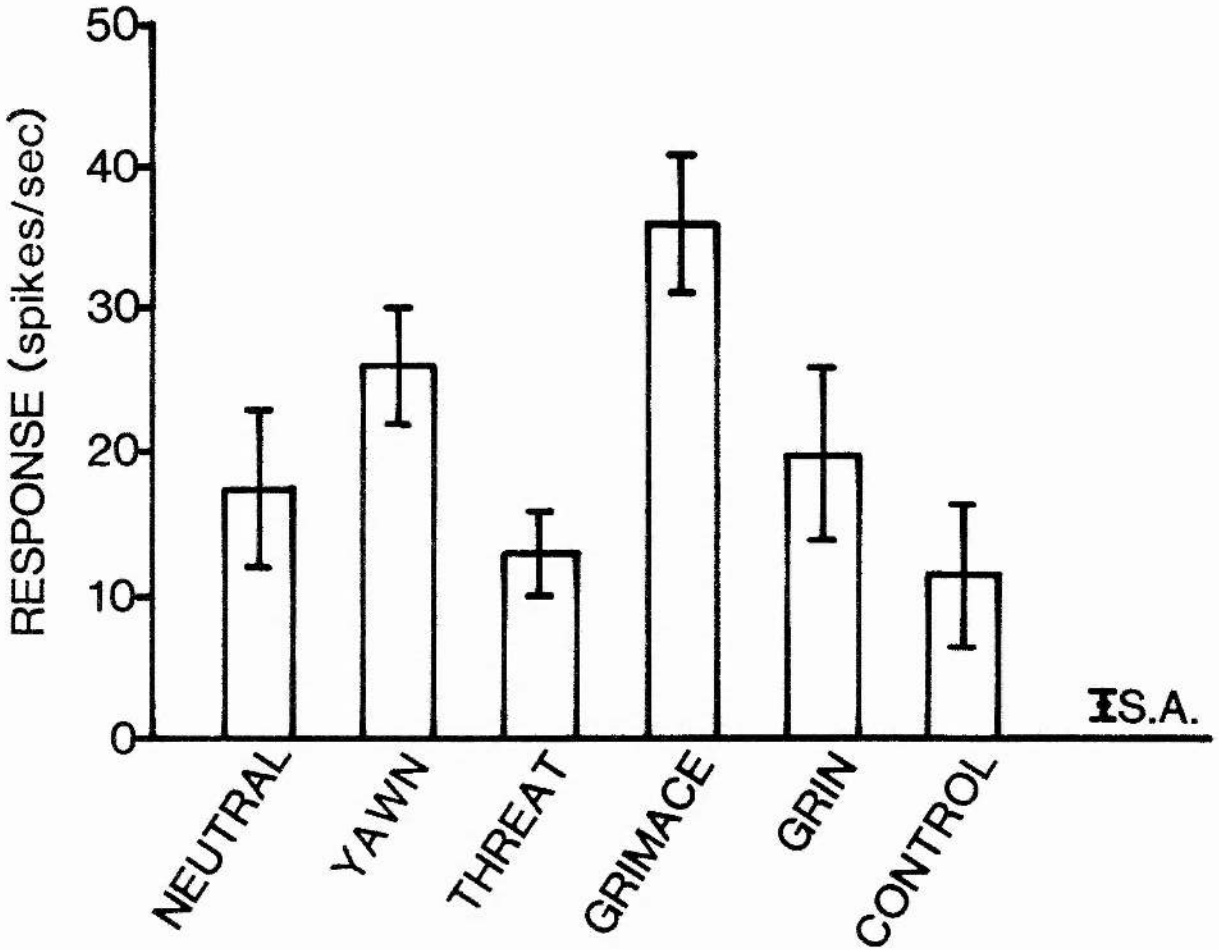


Figure 7.12 Sensitivity to a grimace facial expression. The mean and standard error of response are illustrated for cell F108B. The cell responds most to a grimace, with reduced responses to other threatening and appeasing expressions. S.A., spontaneous activity. (N=6,5,5,5,5,5,6, F=5.3, df=6,30, P<0.01.)

Indications as to the visual basis of expression sensitivity were given by examining the effect of individual parts of the face on the responses of these cells. The majority (5 out of 7 cells) exhibited sensitivity to a particular form of the mouth when presented in isolation. For three cells the response to the mouth alone was equivalent to that of the entire expression; for two cells the response was weaker.

One expression-sensitive cell (F108a) demonstrated an association between the degree to which the mouth was open in an expression and the magnitude of the cell's response. This cell was selective for a yawning face, the response to which differed significantly from that to the other facial expressions - threat and grimace ($p<0.05$), grin and neutral ($p<0.01$) - non-face objects and the cell's s.a. ($p<0.01$ each comparison). These other facial expressions did elicit significant responses when compared with the cell's s.a. ($p<0.01$ each comparison). Ranking the expressions by comparison, with respect to the degree the mouth was open, from neutral (closed mouth) through grin, grimace and threat to yawn (fullest open mouth), revealed a positive correlation of 1.0 ($p<0.01$, Spearman rank correlation coefficient) between this variable and the cell's response magnitude.

Another cell was additionally affected by the presence of teeth. Figure 7.13 shows that when no teeth were visible, the response to open mouth was greater than to a half open mouth ($p<0.05$), but with teeth present the response to a half open mouth did not differ significantly from the open mouth (no teeth). Comparably a half open mouth with no teeth present elicited no significant response in

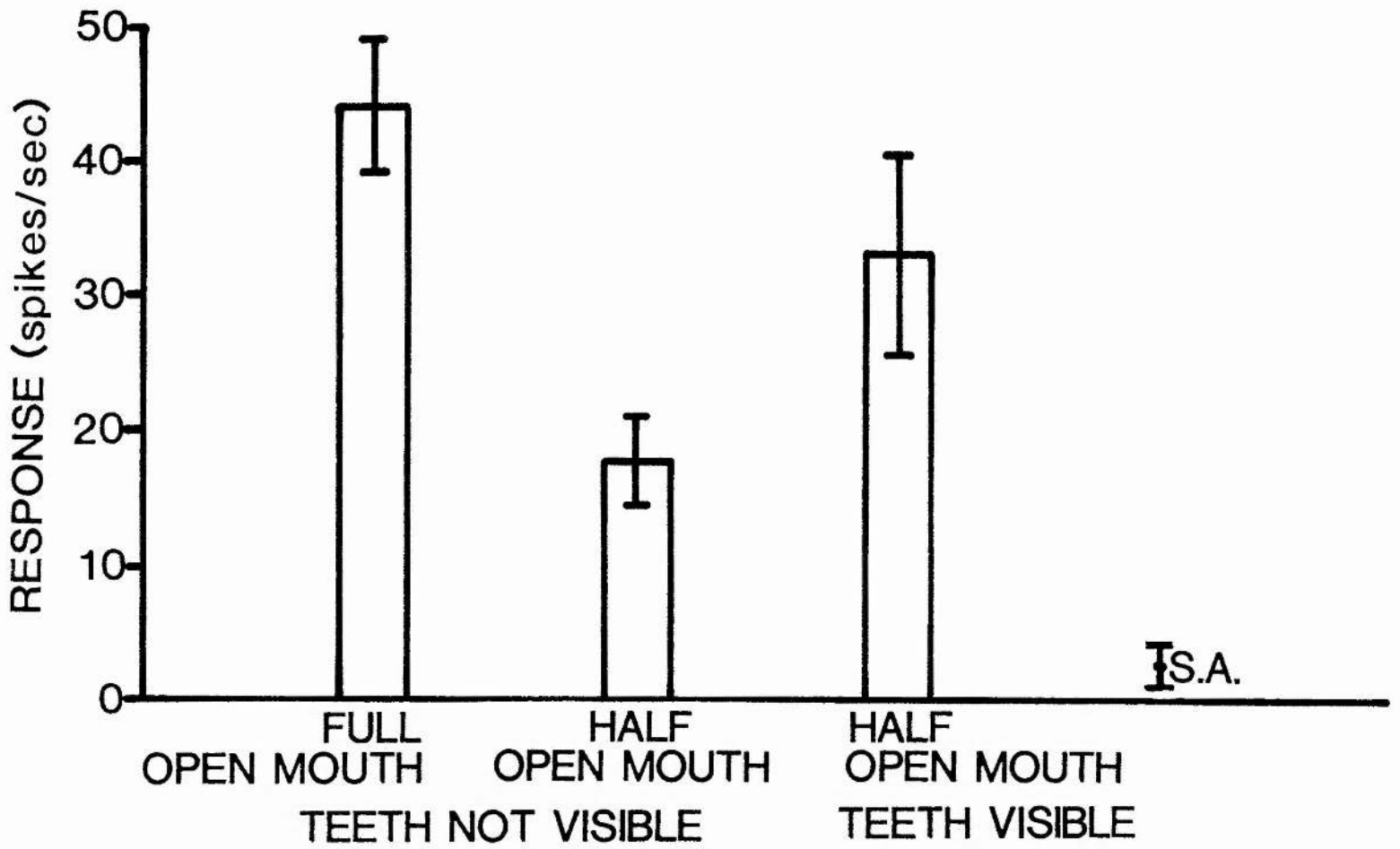


Figure 7.13 Response of a cell (F077C), sensitive to the yawn and threat expression, to individual elements of these expressions. The cell responds more to a full open mouth than a half open mouth; the response to the latter being increased when teeth in the mouth are visible. S.A., spontaneous activity. (N=4, F=11.6, df=3,12, P<0.01.)

comparison with the cell's s.a., whereas open mouth (no teeth) and half open mouth with teeth did ($p<0.01$ each comparison). This suggests then that the open mouth defined sensitivity to the yawn expression facilitated by the presence of teeth.

The direction of eye gaze (as well as the mouth shape) was important for one cell (F077b) selective for yawn and threat (Figure 7.14). This cell responded more to a threat expression where eye contact was made with the subject monkey than to an expression of threat with the eyes averted ($p<0.05$). The response to threat with eye contact was also larger than that to the other expressions all with eye contact ($p<0.01$ each comparison except grimace, $p<0.05$) and the cell's s.a ($p<0.01$). Again, evidence suggested that the degree to which the mouth was open affected the cell's response as threat eye contact (full open mouth) elicited a greater response than a chewing face with a half open mouth ($p<0.05$). A small response was seen to open mouth presented in isolation.

Also noted at the time of the experiment were two cells sensitive to threat that gave a small response to the eyebrows when they were raised from their normal position. Raised eyebrows constitute a further component of the threat face.

Besides the facial elements, the posture of the head itself would seem to make an important contribution in defining a compound facial expression or gesture. The responses of one cell (F105) for which head posture was important are illustrated in Figure 7.15. With a neutral expression the cell gave a significantly greater response

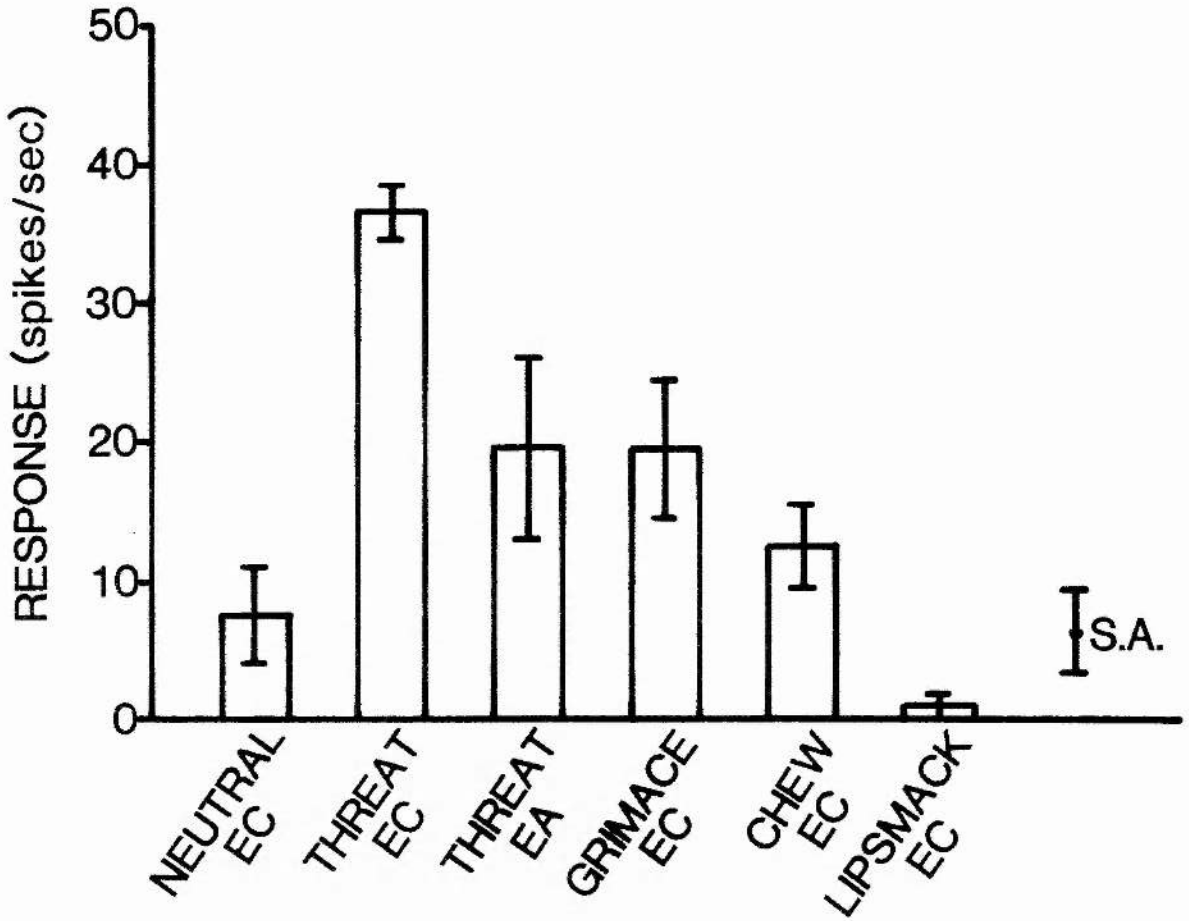


Figure 7.14 Response of a cell (F077B), sensitive to threat expression, to direction of eye gaze. The cell responds more to a threat face with eye contact (EC) than to faces with the same expression but eyes averted (EA) or any other expressions with eye contact. S.A., spontaneous activity. (N=4, F=9.8, df=6,17, P<0.01.)

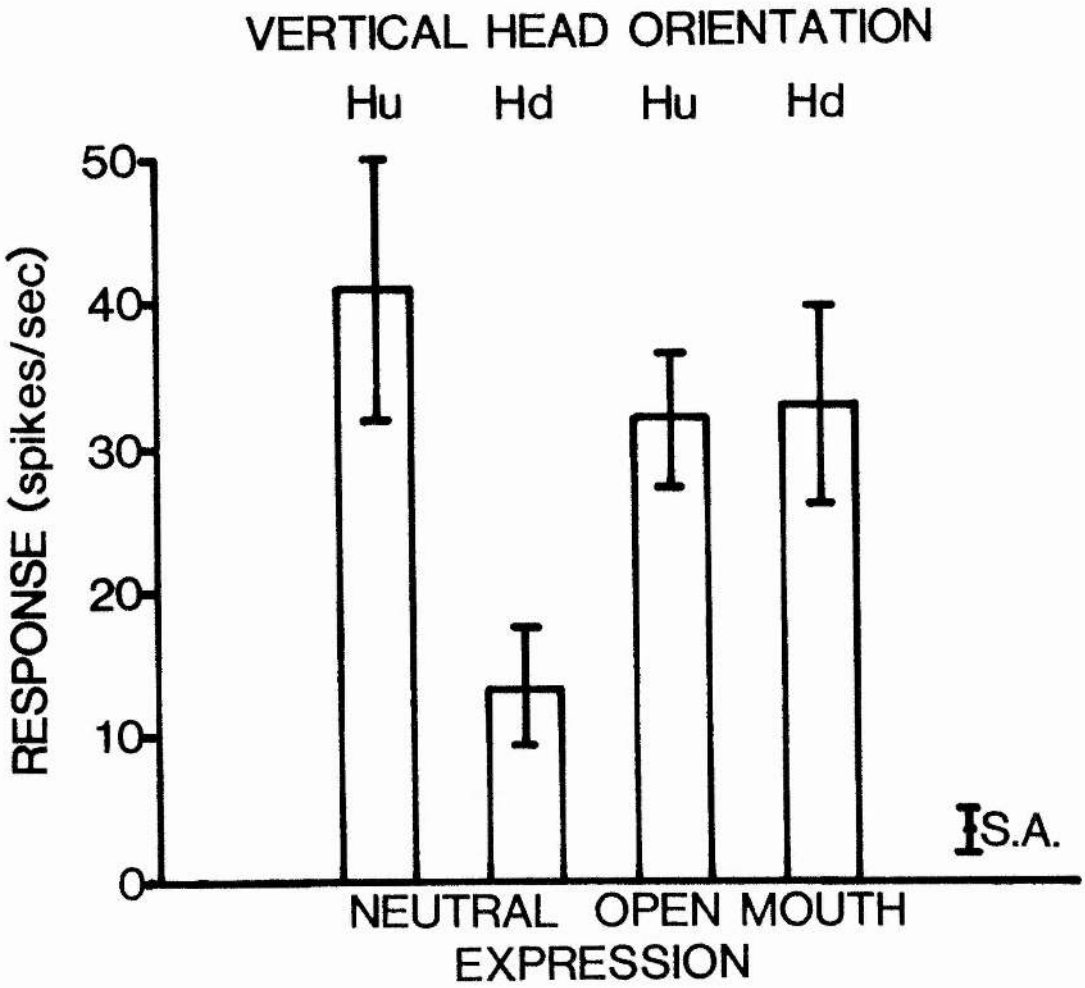


Figure 7.15 Interaction of vertical head orientation and facial expression. With an open mouth facial expression no sensitivity to vertical head orientation is revealed; but with a neutral facial expression the cell (F105) responds more to the head up (Hu) orientation than the head down (Hd). S.A., spontaneous activity. (N=3,2,3,3,3, F=11.0, df=4,24, P<0.01.)

($p<0.01$) to the head oriented up as compared with the head oriented down. This was not true with an open mouth expression where no significant difference in the cell's response to the two head orientations was noted. Interestingly, both the head up and head down open mouth expressions elicited significantly larger responses than the head down neutral expression ($p<0.05$ each comparison).

So, the head up orientation despite expression and the head down orientation with open mouth expression elicited significant responses compared with the cell's s.a. ($p<0.01$ each comparison), but the head down orientation with a neutral expression did not. This suggests an interplay of expression and posture sensitivity whereby head orientation may be utilized at the cellular level to aid the characterization of an expression.

7.3.4 Posture sensitivity

This section of results explores the sensitivity of single cells to the sight of head and body postures both independently and conjointly. There were 18 cells recorded that favoured one whole body posture over another, discriminating between bipedal, quadrupedal or crouch (sitting) postures - some principal postures adopted in the monkey. The relative importance of the different regions of the whole body are described for these cells. A further 16 cells sensitive to the head oriented in the vertical plane are considered in a separate section for clarity.

(a) Body posture

The most commonly encountered group of cells under this classification were activated by the sight of a monkey or human in a quadrupedal posture (10 cells). The responses of the cell (P108) typical of this type of neurone is illustrated in Figure 7.16A. The activity of this cell was affected by the posture of the head and body (in its entirety), the response magnitude being larger to a quadrupedal posture than either a bipedal or crouch posture ($p<0.05$ each comparison), or the cell's s.a. ($p<0.01$). For this cell and for all the cells sensitive to quadrupedal posture the horizontal orientation of the whole body with respect to the subject monkey, i.e. frontal, profile or rear view, was unimportant. This is illustrated for another cell (F067) in Figure 7.16B. Seven cells were selectively responsive for the quadrupedal posture independent of the vertical orientation of the head, indicating that this sensitivity to posture could not be accounted for in terms of head orientation alone.

Three posture-sensitive cells showed an additional preference for a specific vertical head orientation, namely head down. One such cell (P099) is illustrated in Figure 7.17. The cell's responses to a quadrupedal body with the head down and with the head occluded were significantly greater than those elicited by either a quadrupedal body with head oriented up, a bipedal body with the head down, the head oriented down (presented alone) or non-face/body objects and the cell's s.a. ($p<0.01$ each comparison). There were no other significant differences.

Specific comparisons provide an insight into the visual sensitivity of

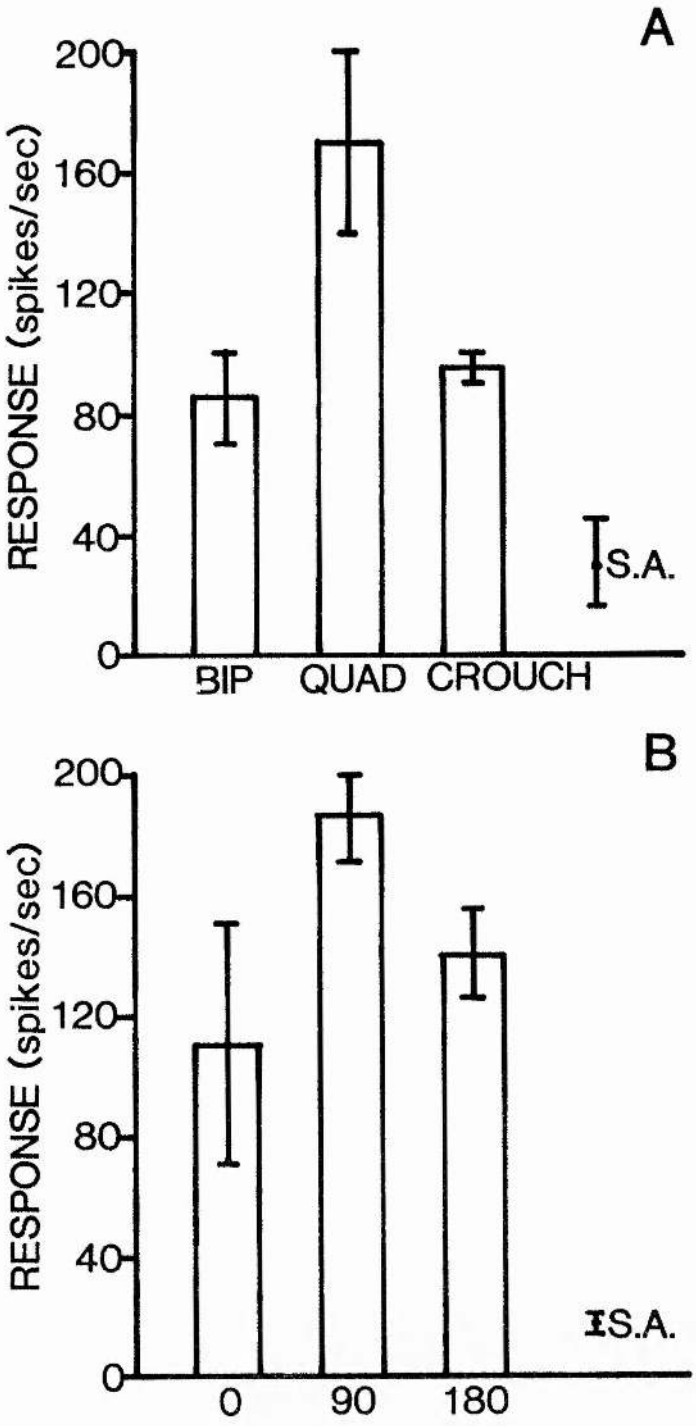


Figure 7.16 Sensitivity to quadrupedal body posture independent of the horizontal orientation of the body. A, the cell (F104) responds most to a quadrupedal (QUAD) body posture, with reduced responses to bipedal (BIP) and crouched (CROUCH) postures. (N=4,6,4,5, F=7.3, df=3,14, P<0.01.) B, for this type of response to a quadrupedal body the cell (F067) gives equivalent responses to the posture regardless of horizontal orientation of the body. 0 (degrees), full face; 90, profile; 180, back of head/body; S.A., spontaneous activity.

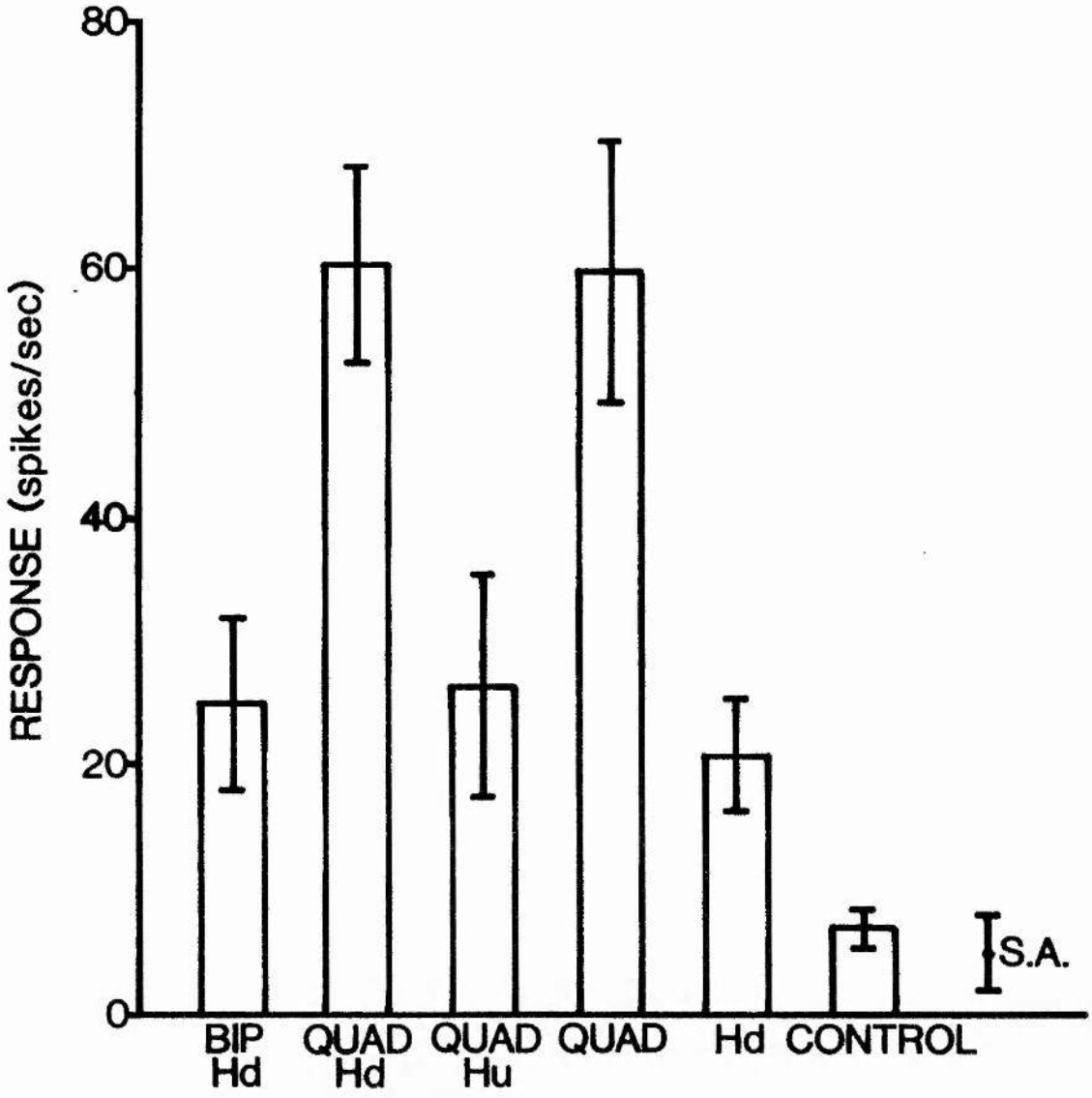


Figure 7.17 Interaction of vertical head orientation and body posture. With the head oriented down (Hd), the cell (P099) responds more to the quadrupedal (QUAD Hd) than the bipedal (BIP Hd) body posture. But, with the head oriented up (QUAD Hu) sensitivity to the quadrupedal posture is reduced. The quadrupedal body alone (QUAD) is sufficient to elicit the cell's response, but the head down orientation (Hd) presented alone is not. Control, non-face/body objects; S.A., spontaneous activity. (N=8,10,8,8,8,10,10, F=12.0, df=6,55, P<0.01.)

this cell. That the cell prefers a quadrupedal body posture is evident from the response elicited by a headless quadrupedal body. Equally, with the same head orientation (head down) a quadrupedal body produced a larger response than the bipedal body. But the cell was sensitive not just to this body posture as a quadrupedal body with the head oriented up did not elicit a response from the cell. Indeed, this non-optimal head orientation actually inhibited the cell's posture sensitivity. The head presented in isolation in a downward orientation was not sufficient either to drive this cell. Such a complex interplay of feature sensitivities at this cellular level do, however, specify quite explicitly a quadrupedal, head down body posture, often associated with threat gesturing.

Just as cells showed a preference for the quadrupedal posture over others, so four cells responded selectively for a bipedal posture. The cell (P073) illustrated in Figure 7.18 demonstrates typical sensitivity to the bipedal posture with response magnitude to the bipedal posture significantly greater than that for a quadrupedal or crouch posture, or the cell's s.a. ($p<0.01$ each comparison). Since the orientation of the head was the same for the upright bipedal and crouched postures, sensitivity to posture here must have been based on parts of the body other than the head. This is reported later in section (b).

Finally, four cells were unresponsive in any posture other than crouch, responding more to this than either bipedal or quadrupedal postures. This is shown for one cell (P102) in Figure 7.19 where the crouch posture elicited a significant greater response than either of

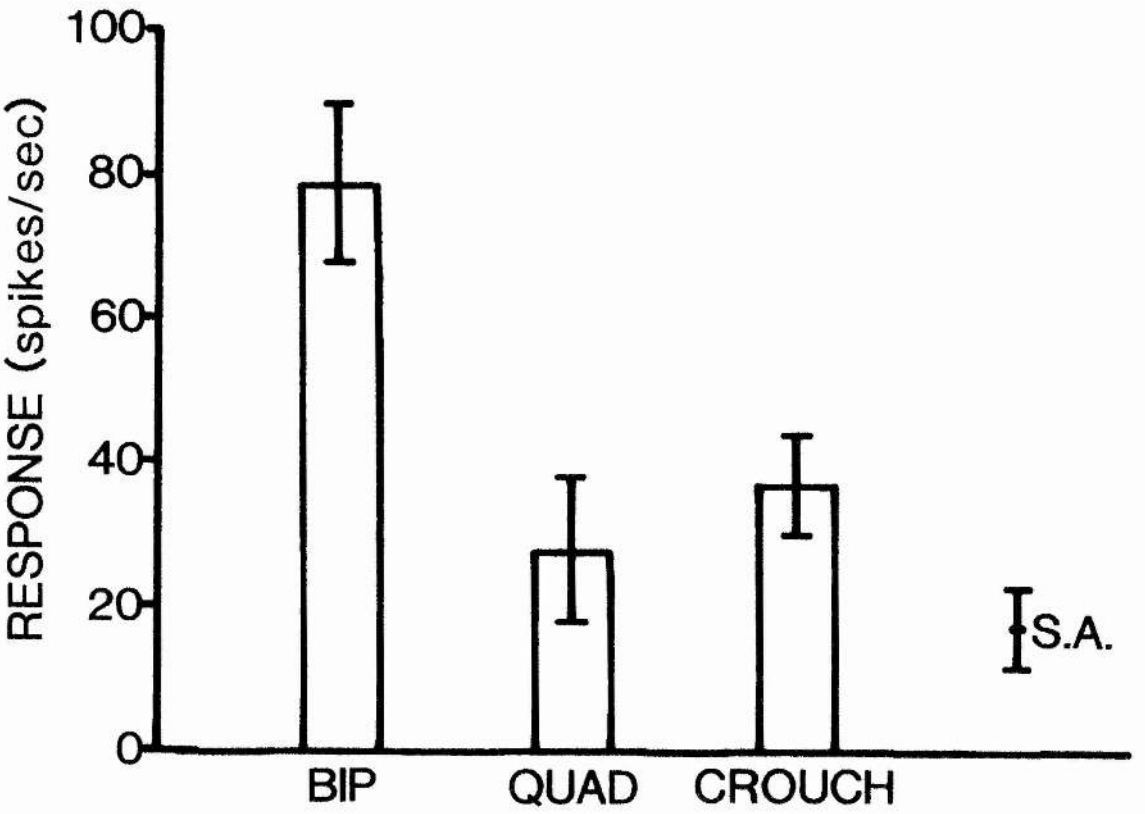


Figure 7.18 Sensitivity to a bipedal body posture. The mean and standard error of response are shown for cell P073. The cell responds more to a bipedal stance than either quadrupedal or crouch postures. S.A., spontaneous activity. (N=5,4,5, F=9.8, df=3,15, P<0.01.)

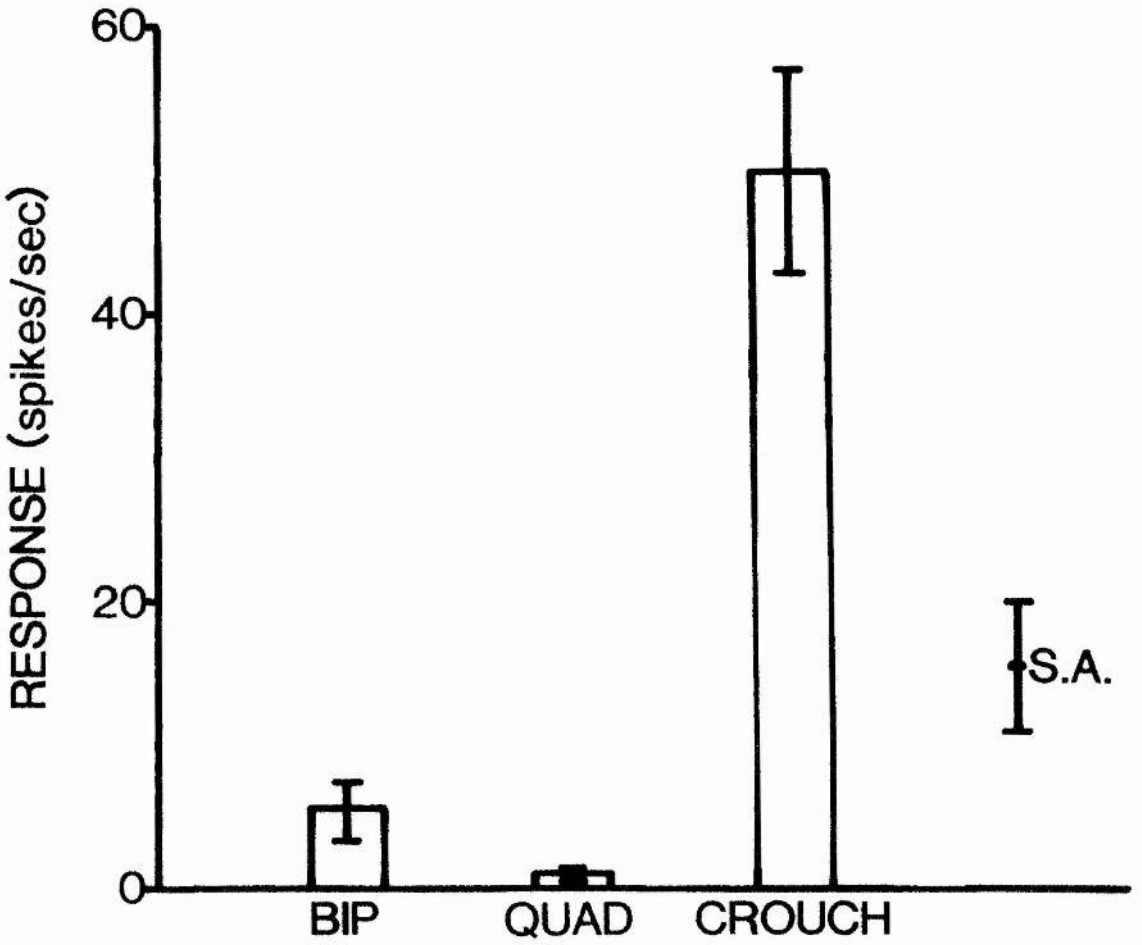


Figure 7.19 Sensitivity to a crouch body posture. The mean and standard error of response are shown for cell P102. The cell responds more to a crouch posture than to bipedal or quadrupedal postures. S.A., spontaneous activity. (N=8,8,10,10, F=21.2, df=3,32, P<0.01.)

the other postures or the cell's s.a. ($p<0.01$ each comparison) and no other significant differences were evident.

Figure 7.20 illustrates for the same cell responses to videotape of monkeys in crouched positions. When the stimulus monkey moved from a crouch to a quadrupedal posture or vice versa, a sharp cut-off was observed in the cell's discharge at the change in posture. Neither a quadrupedal position held by the filmed monkey or a bipedal stance he transferred to produced any significant activity from the cell. The typical response of this crouch-sensitive cell demonstrates that the selectivity for this posture generalized over identity (different monkeys acted as stimuli), view and species - both humans and monkeys in a crouched position could elicit a response from the cell (compare Figures 7.19 and 7.20). Static representations of crouching bodies activated the cell equally well so the responses observed for P102 were not a reflection of dynamic aspects of the stimuli but were attributable to the form of the body at each moment in time.

Seven cells responded to regions of parts of the body presented in isolation. For over half of these cells (4 of 7 tested for sensitivity to parts of the body) responses to more than one body region were as large as the response to the whole body. For the remaining cells (3 of 7) a greater response magnitude was observed to the whole body posture than to component body parts presented in isolation.

One cell (P053) sensitive to a bipedal posture illustrates the latter condition (Figure 7.21A) where the whole body elicited a significantly

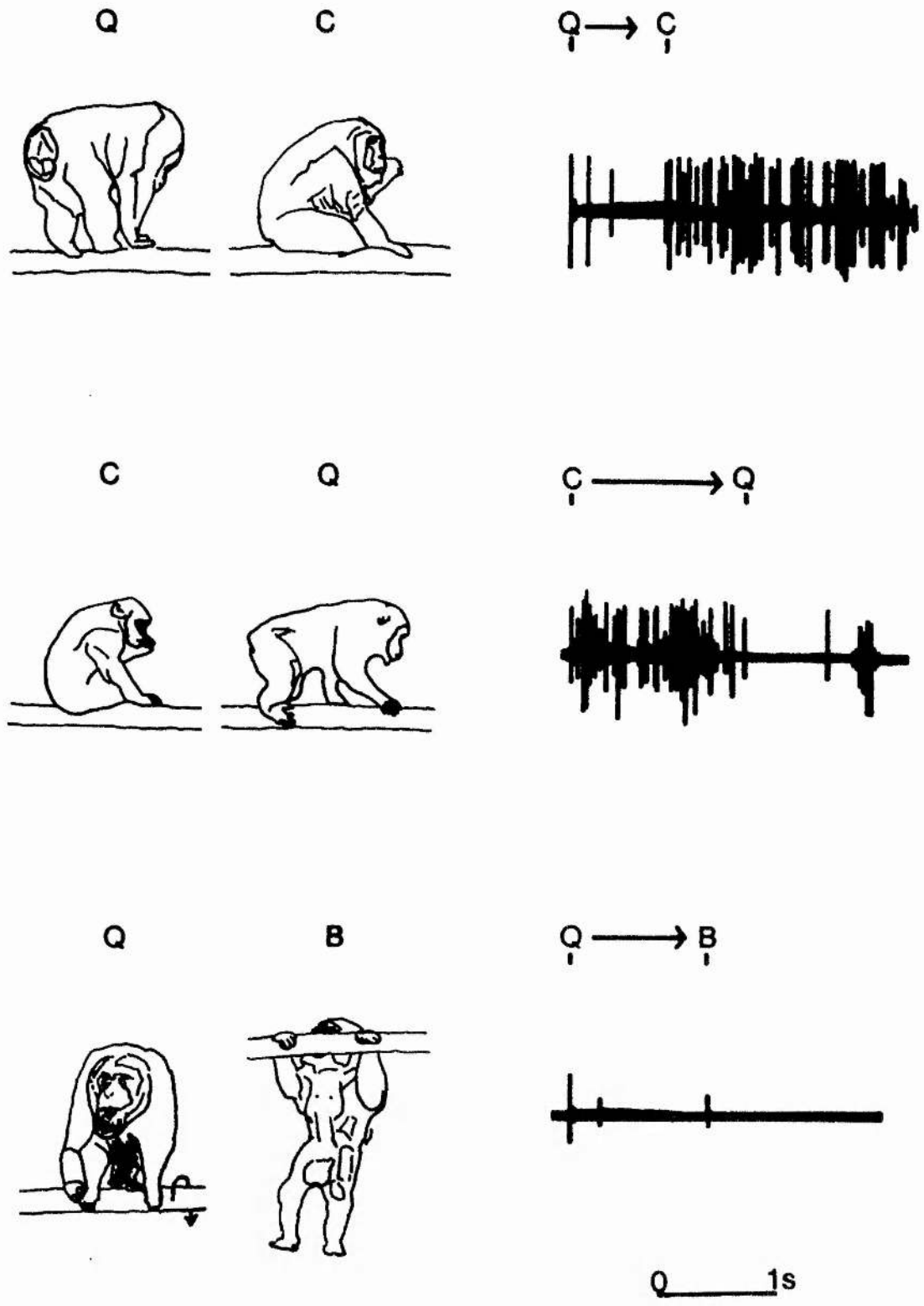


Figure 7.20 Sensitivity to monkeys' crouch body posture. Left column illustrates a video set of dynamic posture changes of rhesus macaque monkeys used as stimuli: Quadrupedal (Q) to crouch (C), movement left to right; C to Q for a second monkey, movement right to left (reversed in the figure); and Q to bipedal (B), movement down from crouch on a tree branch. Right column illustrates recordings of the spike activity of one cell, F043, during presentation of the stimuli. Changes in body posture of the video image are indicated above the spike traces; the calibration bar indicates 1s of neural activity.

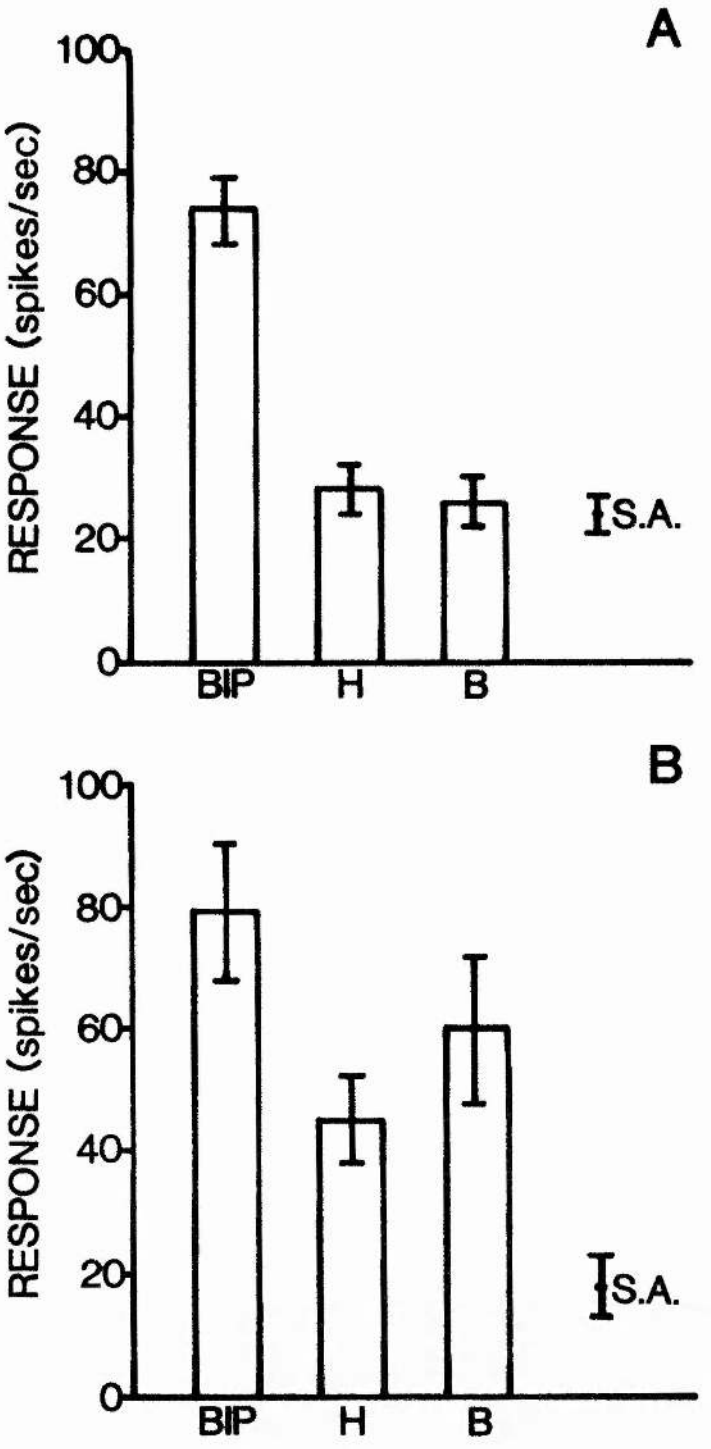


Figure 7.21 Responses of two cells, sensitive to bipedal body posture, to individual elements of the body. A, the response of the cell, P053, to the head alone (H) and the body alone (B) is reduced compared to its response to the whole bipedal body posture (BIP). (N=9, F=32.4, df=3,32, P<0.01.) B, the response of this cell, P073, to both the head alone and the body alone, bipedally oriented, is equivalent to that for the whole bipedal posture. (N=6, F=7.2, df=3,20, P<0.01.) S.A., spontaneous activity.

greater response than either the head alone (body occluded) or the body alone (head occluded) and the cell's s.a. ($p<0.01$ each comparison). Another cell, P073, (Figure 7.21B) demonstrates that individual body regions could elicit an equal response to the whole body. No significant differences in response were found between the whole body, the head or body alone.

(b) Head posture in the vertical plane

A total of 16 cells were identified that responded selectively to the head oriented in the vertical plane. Eight cells responded to the head down (head turned 45 degrees down from the full face), four cells to the head up (head oriented 45 degrees up from full face) and four cells responded to both head up and head down. These cells were generally responsive to the vertical head posture regardless of the horizontal orientation of the head, i.e. all the cells responsive to the full face with head down, for example, were also noted to respond to profile head down and back of the head with the head down.

Two exceptions were found to be responsive to only one head orientation in both the vertical and horizontal planes: One was selective for profile head down and one for profile head up. The responses of one cell (P106) sensitive to the head oriented down and those of another (P106A) sensitive to the head oriented up are illustrated in Figure 7.22A and B respectively. For both cells the optimum stimulus (head down, A; head up, B) give greater responses than the head oriented to other views.

Apart from these two cells, the majority (sensitive to vertical head

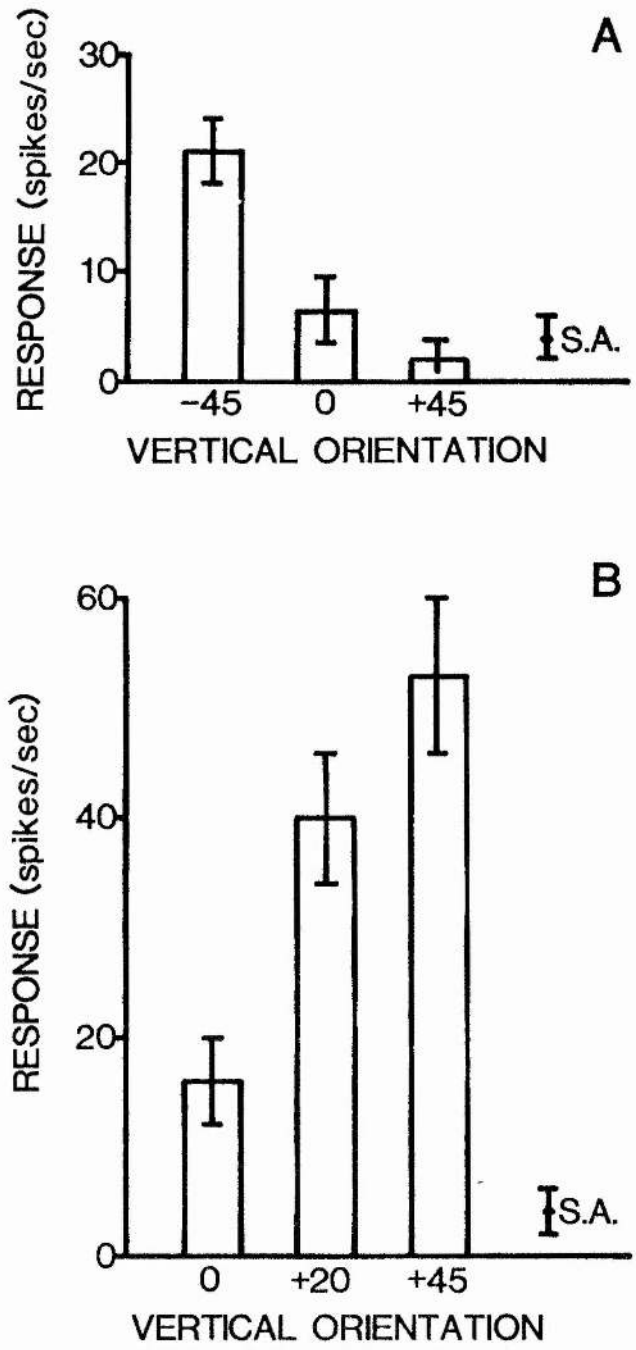


Figure 7.22 Sensitivity to head posture. The mean and standard error of response are illustrated for cell P106 (A) and P106A (B). A, the cell responds more to the head oriented down with respect to the observer (-45 degrees), than to full face (0) or the head raised up (+45). B, the cell responds with an increased firing rate as the face is rotated up from full face to face raised 45 degrees. S.A., spontaneous activity. (Adapted from Perrett et al, 1984, 1985b.)

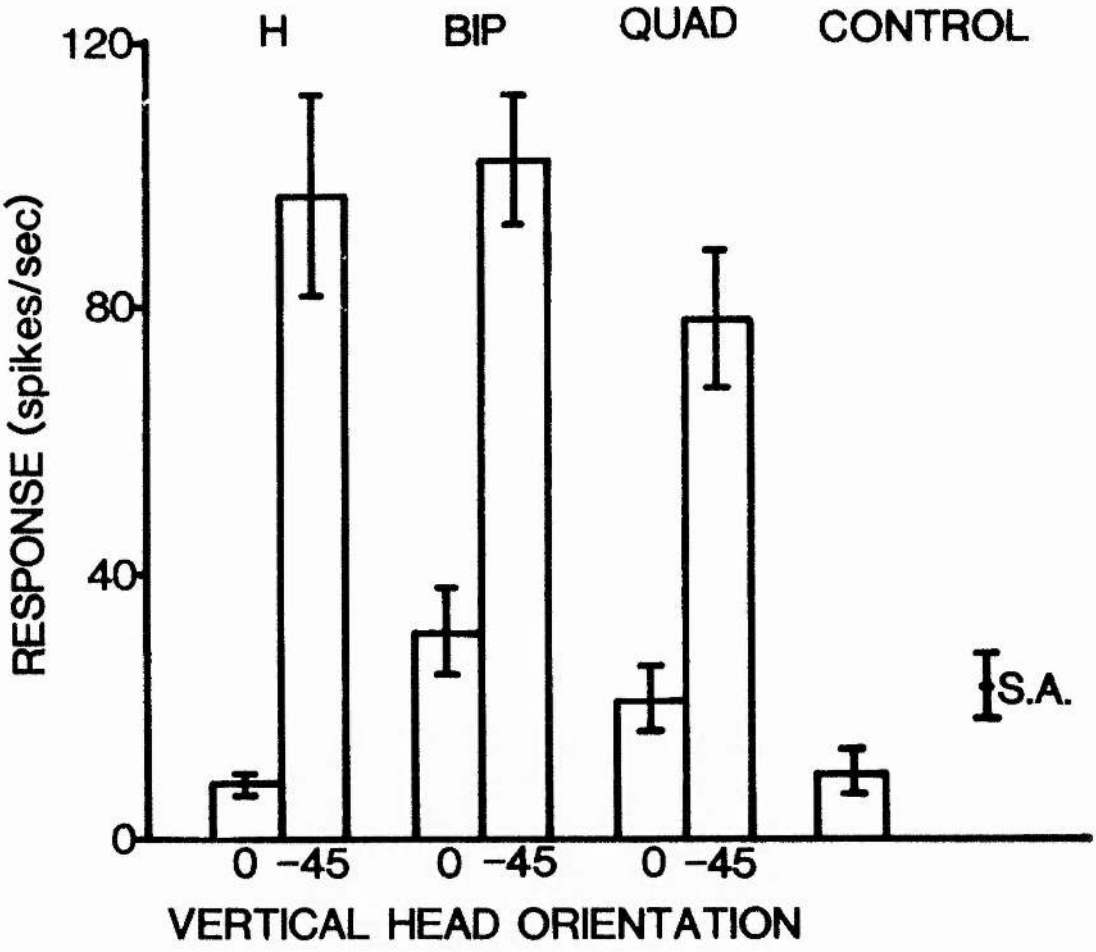


Figure 7.23 Sensitivity to head posture irrespective of body posture. The mean and standard error of response are illustrated for cell P090. The cell responds more to a head down orientation (-45) than to a full face (0) regardless of whether the head alone is shown (H) or whether the head posture is incorporated with a bipedal (BIP) or quadrupedal (QUAD) body posture. Control, non-face/body objects, S.A., spontaneous activity. (N=7,7,7,6,6,7,7,7, F=18.4, df=7,46, P<0.01.

orientation) did not specify head orientation with respect to the viewer. They afforded an object-centred description of the head down posture as illustrated by one cell (P090) in Figure 7.23. Here, the cell responded to the head oriented down regardless of the body's posture. Each head down condition (with the head only, a bipedal or quadrupedal posture) elicited a significantly greater response from this cell than the head oriented at full face with the viewing monkey, or the cell's s.a. ($p<0.01$ each comparison). The responses elicited here were therefore governed by the head oriented down with respect to the body rather than the viewer.

7.4 Discussion

In an attempt to identify the neural mechanisms underlying certain aspects of social communicative behaviour a detailed study was made into the stimulus selectivity of visual neurones (in the cortex of the STS in the temporal lobe) to characteristic monkey facial expressions and head and body postures. The results of this systematic study are discussed in the remainder of the chapter, along with their implications for a neural mechanism underlying visual communication in which the STS cortex appears to play an important role.

7.4.1 Socially important information about the face and body

(a) Facial expressions

Examining the selectivity of face-sensitive cells for facial expressions revealed seven cells that were preferentially activated by a particular form of expression. Four cells responded best to a threat (or yawn) expression, one cell to a yawn expression, one to an open mouth with teeth visible and one cell to a grimace, when tested with a series of threatening, submissive and neutral expressions. (A representative sample of the expressions observed most commonly in the macaque monkey's repertoire (Bertrand, 1969; Hinde and Rowell, 1962; van Hooff, 1962) were employed as stimuli.) Other expressions were not found to be specifically coded for here but only a small population of expression-sensitive cells was investigated.

Some of the cells selective for a threat or yawn expression demonstrated a general selectivity for full open mouth (which is considered in a later section) hence the combined sensitivity to the two expressions. The initial stages of yawn strongly resemble a threat and both expressions can be used as threat gestures, hence these expressions may share a common interpretation. It could be that these expressions are only distinguished by their dynamic qualities, being ambiguous in static pose (Eibl-Eibesfeldt, 1970).

It's critical to state at this point though that for many of the cells the stimulus expression was provided by a human experimenter rather than a monkey. Since there is a dramatic difference in the facial musculature and mechanical structure of human and monkey faces it was impossible for the experimenters to imitate 'perfectly' some of the monkey expressions, hence the subject monkey may have been unable to discriminate between such expressions as threat and yawn as performed

by a human face.

Additionally a yawn is emphasized (especially in adult males) by the size of the canines (Chalmers, 1979) - a difficult feat to reproduce naturally by any experimenter! Similarly, monkey grimace and grin expressions may not have been distinguished by the viewing monkey when imitated by an experimenter. However, a human grin (with no teeth bared) was more often used as a stimulus. Still, the mouth shape and presence of teeth are not the only facial attributes to define an expression; the relative contribution and interdependence of other cues available for the identification of expression may reduce the expressions' ambiguity. These are subsequently described in section 7.4.2.

Cells demonstrated selectivity amongst expression only when the stimulus face was oriented directly towards the subject monkey. Rotation of the head in the horizontal plane to profile or to the back of the head (quite naturally) reduced or eliminated the cells' responses. Expressions in communicative behaviour are part of a shared code in social interactions (Steklis and Raleigh, 1979) and as such the partners in an interaction benefit most by facing each other. Macaques are particularly 'eye-conscious' (Bertrand, 1969; Perrett et al, 1984b) in social encounters where maintained stare or eye aversion alone can signal either a threatening or submissive gesture (Bertrand, 1969; Chalmers, 1979; Chance, 1962; Hinde and Rowell, 1962; van Hooff, 1962). With more propensity for forward-facing expressions (relative to the observer) it is no surprise that the cells sensitive to expression also display selectivity for the frontal view of the face.

On the other hand, for full comprehension of a social situation monkeys may need to be cognizant of the interactions between any pair of individuals and they may be required to characterize a gesture or expression from an alternative view (i.e. with the expressing monkey's face turned to profile to the observer). In the current study one cell did continue to discriminate between threat and neutral faces for profile view; a second neurone sensitive to yawn also responded when the yawning face was oriented directly at the monkey or turned to profile. Hence it seems that coding of expressions can generalize across horizontal orientation even though the visual information from, for instance, a profile threat face must differ considerably from that of a full face threat. A possible explanation for the lack of cells sensitive to expression in any view other than full face might be that profile expression-sensitive cells constitute a separate neural population. This functional organization would then parallel that exhibited by cells sensitive to identity (Perrett et al, 1984, 1987b) which are found both amongst populations of cells tuned to the full face view and separately to cell populations tuned to other views of the head such as the profile.

Expression-sensitive cells' responses tolerated a variety of stimulus parameters. Although most cells were activated best by real three-dimensional stimuli (human faces), some units were observed to give an equivalent response to videotaped film of monkey expressions. From the latter medium it was notable that cells were sensitive to static (or dynamic) aspects of facial expressions and that the responses to a preferred expression were not affected by a number of conditions that could change the appearance of the face such as

lighting, distance from the subject and stereoscopic depth (three-dimensional and real to two-dimensional and videotape). Earlier studies have shown that cells in the STS responsive to the sight of the face per se are unaffected by such 'simple' variables as retinal position (Bruce et al, 1981), distance and size, face colour and orientation (e.g. Perrett et al, 1982, 1984, 1985b).

Perhaps more remarkable is the fact that these cells responded to the preferred expression presented by different species and individuals. A reciprocal observation to this generalization over identity for expression-sensitive cells was made for cells sensitive to face identity that were unaffected by expression (Perrett et al, 1984, 1987b). To code for expression (or identity) brain mechanisms must be able to be selective for expression and capable of generalizing over low order variables (size etc.) and other facial attributes (high order variables) such as identity or species. This division of labour, i.e. deduction of expression regardless of identity and vice versa, conforms to models of human face recognition (e.g Hay and Young, 1982) constructed from behavioural studies.

(b) Body posture

Neuronal sensitivity to body posture has not been studied extensively. In the present study 18 cells were identified with selective responses for one of three characteristic monkey postures - bipedal, quadrupedal and crouched stances. These were selected as representative of the three major postural stances observed in the macaque monkey's behavioural repertoire (Bertrand, 1962; Hinde and Rowell, 1962). These authors describe numerous resting or sitting postures from which

it is clear that the posture described here as a crouch stance was not easily discernable from a hunched sitting position. Again, human posturing could not replicate exactly the nuances of monkey body posture but it did serve as a useful guide to the cells' postural selectivity.

The majority of cells sensitive to posture gave a preferential response to a quadrupedal body, the remainder responding selectively for either a bipedal body or a crouched (or sitting) body. For each cell only the preferred body posture elicited a significant response and in a similar vein to the expression-sensitive cells this response was maintained through a number of viewing conditions. The cells' responses were unaffected by lighting or stimulus size and generalized over species (human and monkey) and identity.

The horizontal orientation with which the posture was presented to the viewing monkey (i.e. facing towards, in profile, or away from the monkey) was not observed to affect the cells' selectivity for posture. Since the preferred body posture activated the cell regardless of its orientation with respect to the viewer, the posture-sensitive cells can be understood as object-centred descriptions (Marr, 1982) of a quadrupedal, bipedal or crouching body. Marr (1982) defines the object-centred description as one which holds for different vantage points (and the viewer-centred description as one which is specific for a given vantage point).

The majority of the cells sensitive to the body's entire posture gave their best responses to real three-dimensional stimuli (human

experimenters) but a few cells did respond equivalently to humans and videotapes of monkeys. For expression it was noted that the dynamic information about the gesture might be essential for its correct characterization. Posture by contrast can be unambiguously recognized from static views which may explain the relatively larger number of cells that could be characterized as posture sensitive.

The question may be raised of whether selectivity for whole body posture could arise from sensitivity to head view alone? Two facts seem to discount this view. First, in the bipedal and crouch postures the head/body angle is essentially the same, yet cells were differentially sensitive to these two postures; second, presentation of the preferred body posture with the head obscured still elicited a good response from a number of cells. That is not to say that the head view or head/body angle is not important to the perception of overall posture (see below and 7.4.2) just that for most posture-sensitive cells visual information from other regions of the body is equally or more important.

(c) Head posture in the vertical plane

Head posture, when oriented in the vertical plane, is yet another element of expression (van Hooff, 1962) that aids the characterization of a compound facial expression. Cells in the STS have previously been identified (Perrett et al, 1985b) that code 'head up' and 'head down' views. In the present study a small population of cells was observed which were selectively responsive to the vertical orientation of the head, independent of body orientation or facial expression. (Those cells that were additionally sensitive to these elements are

discussed in 7.4.2). Half of the cells preferred the head angled down from the viewer (associated with threatening gestures), one quarter of the cells preferred the head angled up from the viewer (associated with submissive gestures), and the remainder were responsive to both head up and head down but were not responsive to full face. The sensitivity of these latter cells was not easy to explain, perhaps they were coding head averted from the viewer - this would however be dependent on the cells responding to a profile face also.

Consistent with the other STS neurones, the head posture-sensitive cells generalized over viewing conditions, namely lighting, size of stimulus etc. Unlike the expression-sensitive cells these cells were unaffected by a change in the horizontal orientation of the head. The majority of cells responded to the preferred elevation of the head for any view in the horizontal plane (e.g. full face head down, profile head down and back of head, head down). Thus the cells cannot be considered to be providing a completely viewer-centred description of head down (Marr, 1982) because the cells generalize across vantage points. Since the cells can also generalize across torso angles (e.g. bipedal or quadrupedal posture) the cells cannot be providing a true object-centred description either . This would require a definition of the head angle relative to the axis of the torso. Perhaps a more appropriate characterization would be a gravity or viewer-referenced description such that the head is lowered with respect to gravity or the viewer.

Two cells were an exception to this characterization as they responded only to one orientation in both the vertical and horizontal planes -

one cell was selective for profile head up and one for profile head down. They can be termed viewer-centred descriptions as the cells' responses were dependent on the angle of the head relative to the viewer. Perrett et al (1984, 1985a) explain how viewer-centred descriptions can be combined to give a comprehensive viewer independent (object-centred) description of the head.

There are a multitude of cues to the head up and head down postures that these cells may utilize: The sight of an extended or fore-shortened neck; the amount of hair visible; the change in pattern of the facial features; or the angle formed between the main axis of the head and body. For object-centred descriptions the latter information would be essential, the other cues being more important for viewer-centred descriptions. Further research would be needed to define which cues contribute to which types of description.

7.4.2 Visual basis of sensitivity

What are the features of a face (head) or body upon which expression and posture sensitivity are based? Are all elements of the face and body of equal importance or do some attributes command more attention than others? The answers to these questions lead us to consider the synthesis of information that transpires at the level of the temporal cortex.

Two systems of operation seem to function concurrently in the STS cortex for both the expression and the posture-sensitive cells. For

one population of cells the combinatorial aspect of several features of a facial expression or body posture elicited a much greater response than any of the parts presented separately, yet single elements could elicit some response from these cells. So it is true to say that for this cell type the whole stimulus was greater than the sum of its parts. This mode of response was exhibited by two expression-sensitive cells and three posture-sensitive cells.

For two yawn/threat-sensitive cells the presence of the mouth alone in appropriate expression (fully open with no teeth visible) was not sufficient to evoke the maximal response observed with a full threat from such cells and neither was the sight of another expression element, raised eyebrows above the eyes' direct gaze. For two bipedal posture-sensitive cells neither the body or the head presented alone in the preferred posture elicited as great a response as the two parts combined. For both classes of cell a convergence of visual information from the constituent parts of an object was essential for the cell to react maximally to the object these parts characterized, e.g. a threat face or a bipedal stance.

A second neural population, it could be said, demonstrated a lower threshold than the neurones just discussed in that they responded to one or more parts of the preferred expression or posture with the same degree of response as to that elicited by the whole face or body. An example can be drawn from both expression and posture sensitivity. Three cells selectively responsive to a yawn/threat face responded equivalently to the single facial attribute of mouth open, and four posture-sensitive cells gave equivalent responses to the whole body,

the head alone and the body alone (or just the top half of the body alone) if in the preferred posture.

It is hard to fully comprehend the necessity for having two neural populations in the same brain area coding the same stimuli but at different levels of analysis unless the behavioural significance of such analyses is considered. In the natural world, it is rare to be in a situation where all the information about that situation is readily available. It is often the case that one must extrapolate from the information that is accessible. Consider such circumstances as a monkey standing upright behind waist-high dense vegetation or a monkey gesturing to another with the sun throwing a shadow over the top half of its face. In this case judgement would have to be made about the monkey's motive or intent from information about parts of the face or body.

In the latter example maybe only an open mouth is visible to the viewing monkey; by default it would be wise for the viewer to treat this as a direct threat. In truth this gesture may be directed to another monkey as revealed by the direction of eye gaze, or not be an aggressive threat at all but an action more related to the consumption of food. The point being stressed is that at the behavioural level all the information necessary to create a totally unambiguous signal is not always provided. Sometimes a default system of assumptions such as that described, may have to be called into play.

At the neural level if units sensitive to expression could <u>only</u> be fully activated by, for instance, three attributes of a threat face

being present - eye contact, eyebrows raised and mouth open - the cell would not recognize the threat (perhaps being given) in the above situation. The value of both populations of cells can then be recognized. (Note that this does not solve the problem of which cells are activated and used for further processing when all the necessary information is available.)

Disambiguating a signal can come not only from combining internal elements of a signal (e.g. the features of the face, or the limbs and torso of the body) but from utilizing more than one communicative signal such as head posture and expression, or head and body posture. In line with previous studies (Perrett et al, 1984, 1985a,b) cells in the STS have been identified sensitive to faces and bodies, particularly responsive to expression, direction of eye gaze (Perrett et al, 1985b), head posture oriented in both the horizontal and vertical planes and body posture, all of which act independently as effective signals in social behaviour. Neurones exhibiting dual selectivity for these social signals have been identified for which it was impossible to explain the cell's response in terms of one of the signals alone.

One cell responsive to a yawn/threat expression was only so when eye contact was made with the subject monkey. Eye contact with other expressions elicited a much reduced response as did a threat with the eyes averted from the subject monkey (where the open mouth might have afforded an independent signal) so defining quite specifically the cell's response to a threat expression. Likewise, a cell that responded to a head up posture regardless of expression also displayed

a response to the head down if presented with an open mouth expression. Since the threat expression is associated with head down and the yawn expression with head up (Bertrand, 1969; Chalmers, 1979; Hinde and Rowell, 1962; van Hooff, 1962), this cell would appear to be indiating the presence of components of a yawn.

The final example illustrates independent and joint sensitivity for a posture defined by both the head and the body. The cell responded to a head down view (with or without the body in view) and also to a quadrupedal body posture (even with the head occluded). When both head and body postures were available together as cues the orientation of the head proved to be the more salient feature, overriding by its posture the effect of the body. Yet with unified information the cell could define a quadrupedal head down posture which may be associated with a lunging threat gesture. The data from this cell therefore suggest a default value much like that described previously.

Study of the utilization of visual information to establish cellular sensitivity to social communicative postures and gestures has thus indicated that cells can rely on information about more than one region of the face or body and that some cells rely on the overall combination (or configuration) of certain features. The output of such neurones reflects an elaborate convergence of visual information about socially important stimuli through which a single, unambiguous representation of a signal can be achieved.

7.4.3 Other factors to explain sensitivity

Some may argue that the selectivity being witnessed here results from a simpler form of stimulation or that the cellular responses observed do not reflect perceptual processes but emotional ones such as arousal. It would be a formidable task to prove unquestioningly that no other factors could explain posture or expression sensitivity but it is possible to dismiss many of the alternatives.

It is doubtful that the expression and posture-sensitive neurones were actually selective for a simple, local stimulus feature such as a particular length of line, a patch of colour or a certain texture (in a particular retinal location) as each of the neurones responded to a wide variety of faces and bodies but not to other two-dimensional or three-dimensional stimuli. The cells responded to both monkeys and humans over a wide range of sizes presented 'live' or on videotape and under many viewing conditions; it is unlikely that through all these tests a 'simple' stimulus feature could remain the invariant cause of a given cell's response. Indeed, the very nature of the expression and posture-sensitive cells' selectivity contradicts this view as responses to one expression or posture are greater than another in which the component facial or body elements are still present.

Taking for example a threat expression-sensitive cell, could it not be justified to say that the neurones were selective for a specific pattern of shapes rather than a threat face? It seems here that this is a semantic problem rather than a perceptual one as will become clear. It might be argued that the crucial features for the neurone's response were a dark, oval shape (the open mouth) situated below centre in a larger oval (the face). (Although the responses of such

cells were often enhanced by other internal features this might have reflected a texture or further pattern sensitivity.) Yet, as the list of stimulus conditions that elicit a maximal response from the cell increase, they begin to approach a description of the essential features of a threat face. So whether or not one wishes to argue that simpler sensory features can explain the properties of these neurones, at present it seems most appropriate to describe the cells as responding to a facial expression or a body posture. Analogous arguments have been applied to cells apparently selective for hand and faces per se (Desimone et al, 1984; Gross et al, 1972; Perrett et al, 1984, 1985a,b).

Several reasons counter the suggestion that responses of the facial expression and head and body posture-sensitive cells were due to arousal. Very few of these cells responded to intense somaesthetic or auditory stimuli, or visual stimuli other than the preferred stimulus that could elicit emotional reactions from monkeys during the recording procedure. Arousal, general or confined to visual stimuli, could not explain why some cells were selective for facial expression and others for head posture; indeed, why some neurones responded preferentially to a threat expression and others to a grimace.

7.4.5 The role of the STS in communication

How is the STS suited to the role of a mechanism for relating emotional responses to stimuli and is there any evidence from sources other than this neurophysiological investigation that reflect this

apparent function of the STS?

With the discovery of face-sensitive cells in primates and even sheep (e.g. Baylis et al, 1985; Bruce et al, 1981; Desimone et al, 1984; Gross et al, 1972; Leinonen and Nyman, 1979; Leonard et al, 1985; Perrett et al, 1982, 1984, 1985b, 1987b; Rolls et al, 1977, 1985; and Kendrick and Baldwin, 1987) and cells sensitive to movements and the form of the body (Gross et al, 1972; Perrett et al, 1985a, 1987a), primarily in the STS polysensory cortex but also in the frontal cortex and amygdala, it seems apparent that part of the visual processing system is devoted to stimuli that are of particular biological importance to monkeys. Such stimuli must include the expressions, postures and gestures encountered in social interactions.

Indeed, it is not just this lab that have reported cells in the STS preferentially responsive to facial expression (Perrett et al, 1985b and this chapter), others have described very small populations of cells in both the STS cortex, the amygdala and the posterior parietal cortex selectively responsive to a change in expression from neutral to open mouth threat (e.g. Baylis et al, 1985; Leinonen and Nyman,1979; Leonard et al, 1985). Leonard et al (1985) tentatively concluded that their neurones responsive to the 'simple continuum' of expression could reflect emotionality. With demonstrations in the STS cortex of not only facial expression-sensitive cells but head and body posture-sensitive cells and cells responding preferentially to the direction of eye gaze, it can be left in no doubt that some selective processing of 'emotionality' is occurring. The STS is not being proferred as an area of the cortex that mediates emotional response,

but as a perceptual mechanism performing a high level of analysis on socially important communicative elements, outputing information that could then be utilized by other brain areas to mediate appropriate emotional and motor responses to the signals received.

Connectional and ablation studies make up important sources of data concerning the functions of the primate STS. There is a heavy projection from the STS to the amygdaloid complex (e.g. Aggleton and Passingham, 1981), part of the limbic system believed to mediate emotional behaviour (Steklis and Raleigh, 1979) where a stimulus is provided with motivational or emotional significance (Aggleton and Passingham, 1981; Geschwind, 1965; Horel et al, 1975; Jones and Mishkin, 1972; Weiskrantz, 1970). This close association with the amygdala might provide a route via which the visual information from the STS organizing postures and expressions for agonistic behaviour could be translated into appropriate emotional reactive behaviour.

Destruction of either the temporal lobes or the amygdala results in the production of the major symptoms of Kluver-Bucy syndrome (reviewed previously in Chapter 4) which include a compulsive inquisitve reaction to stimuli and striking lack of emotional responsiveness (Aggleton and Passingham, 1981; Bucy and Kluver, 1955; Dicks et al, 1969; Horel et al, 1975; Kling, 1972; Kluver and Bucy, 1939; Weiskrantz, 1956). Specific damage to the STS has revealed both mild and distinct behavioural changes, namely, a general hyporesponsivity to visual and tactual stimuli (Luh et al, 1986); 'fearfulness' after surgery (Ettlinger and Garcha, 1980); and an inability to discriminate between socially relevant stimuli such as expressive head postures and

face versus non-face (Chapter 6).

A sequential processing of visual information from retina through to temporal cortex to the limbic system has been postulated (Geschwind, 1965; Jones and Mishkin, 1972; Weiskrantz, 1970) which implies that the STS and amygdala are sequential steps in this sequence of visual processing. The changes in affective behaviour can be produced by cutting off visual inputs to the amygdala (Downer, 1961) and to some degree by destruction of the STS. If destroying the amygdala cuts off cortical information from brain systems that organize the postures and expressions for social agonistic behaviour (Fernandex de Molina and Hunsperger, 1962; Hilton and Zbrozyna, 1963; Horel et al, 1975) and destroying the STS impairs the ability to discriminate appropriately between socially relevant stimuli, then it follows that the STS may be one region of the neocortex providing the sensory information or visual control for the mechanism mediating emotional responses.

7.4.6 Neural mechanisms for communication

Interestingly, Desimone et al (1984) recall two examples of social communication for which specialized neural mechanisms have evolved: Song in the bird; and language in man. They point out that the location of the supramodal language cortex in man appears to be equivalent to the location of the STS in the monkey. Desimone et al conclude that this area of primate brain may be 'a fertile zone for the development of supramodal mechanisms for communication'.

Neurophysiological evidence from the somatosensory study of STS cells (Chapter 7) and the study of facial expression and head and body posture-sensitive cells (present chapter) in conjunction with behavioural evidence (Chapter 4) emphasizing the change in affective behaviour after removal of the STS, together suggest that the STS is a region of primate brain specialized for social communication in monkeys.

7.5 References

Aggleton, J.P., and Passingham, R.E. (1981) Syndrome produced by lesions of the amygdala in monkeys (Macaca mulatta). Comp. Physiol. Psychol. 95:961-977.

Andrew, R.J. (1963) Evolution of facial expression. Science 142:1034-1041.

Argyle, M. (1975) Bodily Communication. Methuen, New York.

Baylis, G.C., Rolls, E.T., and Leonard, C.M. (1985) Selectivity between faces in the responses of a population of neurones in the cortex in the superior temporal sulcus of the monkey. Brain Res. 342:91-102.

Bertrand, M. (1969) The behavioural repertoire of the stumptail macaque. Bibliotheca Primatologica no.11. Karger, Basel.

Bruce, C., Desimone, R., and Gross, C.G. (1981) Visual properties of neurons in a polysensory area in superior temporal sulcus of the macaque. J. Neurophysiol. 46:369-384.

Bucy, C.P., and Kluver, H. (1955) An anatomical investigation of the temporal lobe in the monkey (Macaca mulatta). J. Comp. Neurol. 103:151-252.

Chalmers, N.R. (1968) The visual and vocal communication of free-living mangabeys in Uganda. Folia Primatol. 9:258-280.

Chance, M.R.A. (1962) An interpretation of some agonistic postures: The role of "cut-off" acts and postures. Symp. Zool. Soc. Lond. 8:71-99.

Darwin, C. (1965) The Expression of the Emotions in Man and Animals. Greenwood Press, London.

Desimone, R., Albright, T.D., Gross, C.G., and Bruce, C. (1984) Stimulus-selective responses of inferior temporal neurons in the macaque. J. Neurosci. 4:2051-2062.

Dicks, D., Myers, R.E., and Kling, A. (1969) Uncus and amygdala lesions: Effects on social behaviour in the free-ranging rhesus monkey. Science 165:69-71.

Downer, J.L. de C. (1961) Changes in visual gnostic functions and emotional behaviour following unilateral temporal pole damage in the split brain monkey. Nature 191:50-51.

Eibl-Eibesfeldt, I. (1970) Ethology: The Biology of Natural Behaviour. Holt, Rinehart and Winston, New York, pp.408-431.

Ettlinger, G., and Garcha, H.S. (1980) Cross-modal recognition by the monkey: The effects of cortical removals. Neuropsychologia 18:685-692.

Fernandex de Molina, A., and Hunsperger, R.W. (1962) Organization of the subcortical system governing defence and flight reactions in the cat. J. Physiol. 160:200-213.

Geschwind, N. (1965) Disconnexion syndromes in animal and man, Part 1. Brain 88:237-294.

Gross, C.G., Rocha-Miranda, E.E., and Bender, D.B. (1972) Visual properties of neurons in inferotemporal cortex of the macaque. J. Neurophysiol. 35:96-111.

Hay, D.C., and Young, A.W. (1982) The human face. In: Normality and Pathology in Cognitive Functions. Academic Press, London, pp.173-202.

Hilton, S.M., and Zbrozyna, A.W. (1963) Amygdaloid region for defence reactions and its afferent pathways to the brainstem. J. Physiol. 165:160-173.

Hinde, R.A., and Rowell, T.E. (1962) Communication by postures and facial expressions in the rhesus monkey (Macaca mulatta). Proc. Zool. Soc. Lond. 138:1-21.

Horel, J.A., Keating, E.G., and Misantone, L.J. (1975) Partial Kluver-Bucy syndrome produced by destroying temporal neocortex or amygdala. Brain Res. 94:347-359.

Jones, B., and Mishkin, M. (1972) Limbic lesions and the problem of stimulus-reinforcement associations. Exp. Neurol. 36:362-377.

Kendrick, K.M., and Baldwin, B.A. (1987) Cells in the temporal cortex of conscious sheep can respond preferentially to the sight of faces. Science 236:448-450.

Kingdon, J.S. (1980) The role of visual signals and face patterns in African forest monkeys (guenons) of the genus Cercopithecus. Trans. Zool. Soc. Lond. 35:425-475.

Kling, A. (1972) Effects of amygdalectomy on social-affective behaviour in non-human primates. In: B.E. Eleftheriou (ed.) The Neurobiology of the Amygdala. Plenum Press, New York, pp.511-536.

Kluver, H., and Bucy, P.C. (1939) Preliminary analysis of functions of the temporal lobes in monkeys. Arch. Neurol. 42:979-1000.

Leinonen, L., and Nyman, G. (1979) Functional properties of cells in anterolaleral part of area 7 associative face area of awake monkeys. Exp. Brain Res. 34:321-333.

Leonard, C.M., Rolls, E.T., Wilson, F.A.W., and Baylis, G.C. (1985) Neurons in the amygdala of the monkey with responses selective for faces. Behav. Brain Res. 15:159-176.

Luh, K.E., Butter, C.M., and Buchtel, H.A. (1986) Impairment in orienting to visual stimuli in monkeys following unilateral lesions of the superior sulcal polysensory cortex. Neuropsychologia 24:461-470.

Marr, D. (1982) Vision: A Computational Investigation into the Human Representation and Processing of Visual Information. W.H. Freeman, San Francisco.

Marriott, B.M., and Salzen, E.A. (1978) Facial expressions in captive squirrel monkeys (Saimiri sciureus). Folia Primatol. 29:1-18.

Penfield, W., and Rasmussen, T. (1950) The Cerebral Cortex of Man. Macmillan Press, New York.

Perrett, D.I., Harries, M., Mistlin, A.J., and Chitty, A.J. (1987a) Three stages in the classification of body movements by visual neurons. In: H. Barlow, C. Blakemore and M. Weston Smith (eds) Images and Understanding. Cambridge University Press, Cambridge (in press).

Perrett, D.I., Mistlin, A.J., and Chitty, A.J. (1987b) Visual neurones responsive to faces. Trends Neurosci. 10:358-364.

Perrett, D.I., Mistlin, A.J., Chitty, A.J., Smith, P.A.J., Potter, D.D., Broennimann, R., and Harries, M. (1987c) Specialized face processing and hemispheric asymmetry in man and monkey: Evidence from single unit and reaction time studies. Behav. Brain Res. (in press).

Perrett, D.I., Rolls, E.T., and Caan, W. (1982) Visual neurones responsive to faces in the monkey temporal cortex. Exp. Brain Res. 47:329-342.

Perrett, D.I., Smith, P.A.J., Mistlin, A.J., Chitty, A.J., Head, A.S., Potter, D.D., Broennimann, R., Milner, A.D., and Jeeves, M.A. (1985a) Visual analysis of body movements by neurones in the temporal cortex of the macaque monkey: A preliminary report. Behav. Brain Res. 16:153-170.

Perrett, D.I., Smith, P.A.J., Potter, D.D., Mistlin, A.J., Head, A.S., Milner, A.D., and Jeeves, M.A. (1984) Neurones responsive to faces in the temporal cortex: Studies of functional organization, sensitivity to identity and relation to perception. Human Neurobiol. 3:197-208.

Perrett, D.I., Smith, P.A.J., Potter, D.D., Mistlin, A.J., Head, A.S., Milner, A.D., and Jeeves, M.A. (1985b) Visual cells in the temporal cortex sensitive to face view and gaze direction. Proc. Roy. Soc. Lond. B. 223:293-317.

Pigarev, I.N., Rizzolatti, G., and Scandolara, C. (1979) Neurons responding to visual stimuli in the frontal lobe of macaque monkeys. Neurosci. Lett. 12:207-212.

Rolls, E.T. (1981) Responses of amygdaloid neurones in the primate. In: Y. Ben-Ari (ed.) The Amygdaloid Complex. Elsevier, Amsterdam, pp.383-393.

Rolls, E.T., Baylis, G.C., and Leonard, C.M. (1985) Role of low and high spatial frequencies in the face-selective responses of neurons in the cortex in the superior temporal sulcus in the monkey. Vis. Res. 25:1021-1035.

Rolls, E.T., Judge, S.J., and Sanghera, M.K. (1977) Activity of neurones in the inferotemporal cortex of the alert monkey. Brain Res. 130:229-238.

Steklis, H.D., and Raleigh, M.J. (1979) Behavioural and neurobiological aspects of primate vocalization and facial expression. In: H.D. Steklis and M.J. Raleigh (eds) Neurobiology of Social Communication in Primates: An Evolutionary Perspective. Academic Press, New York, pp.257-282.

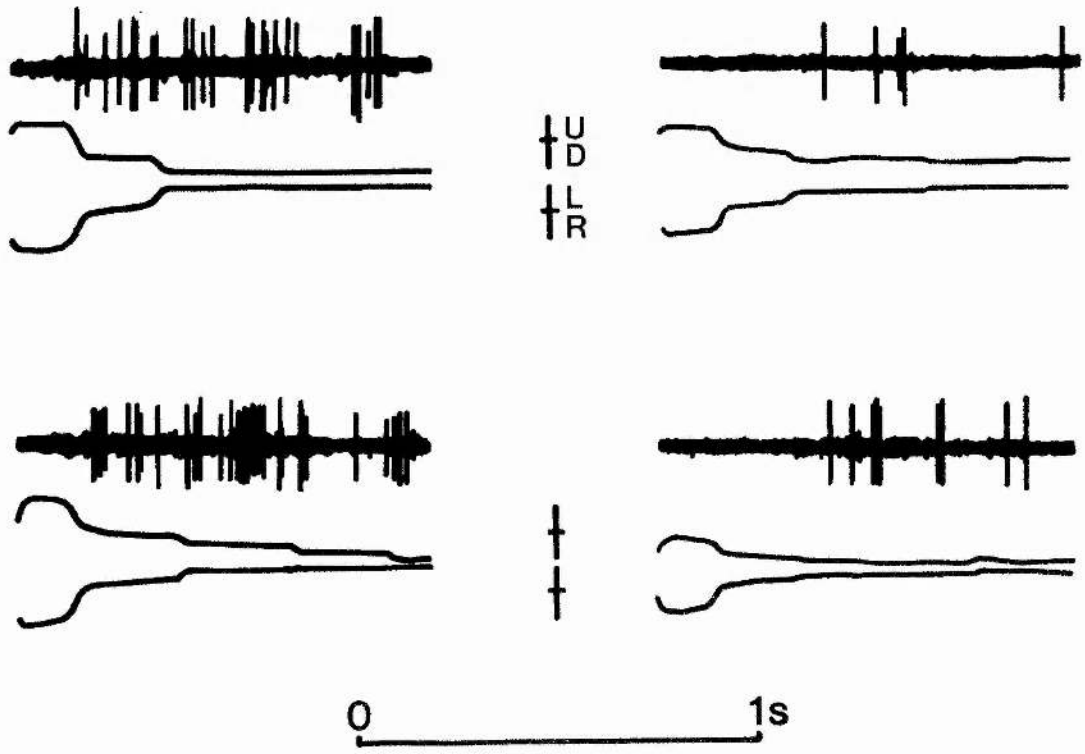
van Hooff, J.A.R.A.M. (1962) Facial expressions in higher primates. Symp. Zool. Soc. Lond. 8:97-125.

Weiskrantz, L. (1956) Behavioural changes associated with ablation of the amygdaloid complex in monkeys. J. Comp. Physiol. Psychol. 49:381-391.

Weiskrantz, L. (1970) Visual memory and the temporal lobe of the monkey. In: R.E. Whalen, R.F. Thompson, M. Verzeano, and N.M. Weinberger (eds) The Neural Control of Behaviour. Academic Press, New York, pp.239-256.

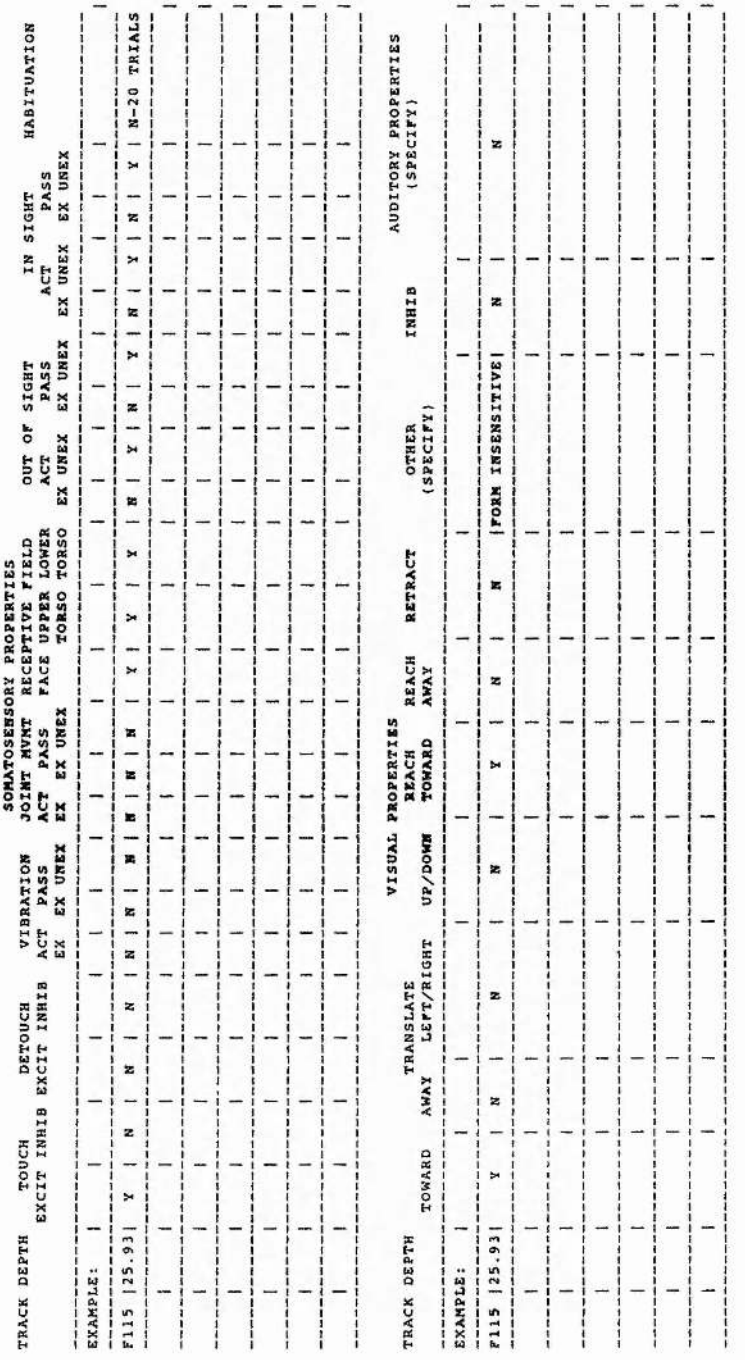
Appendix A

The figures below illustrate two trials with movements of the hand (left column) and control stimuli (right column) towards a target object. For each trial the upper trace represents neuronal activity and lower traces are records of vertical and horizontal eye position monitored simultaneously with an infrared tracking device (ACS). Vertical calibration bars for eye movement = 20 degrees (10 degrees up, U and down, D and 10 degrees left, L and right, R of a position straight ahead). Trial records begin with the onset of stimulus movement. Neuronal responses were not related to patterns of eye movements which are triggered by or used to follow given actions, since qualitatively similar patterns of saccades, tracking and fixations occur despite dissimilar neuronal responses.



Appendix B

The characteristic sensory properties of somatosensory cells in the STS were collated on information sheets as shown below. Key to abbreviations: EXCIT, excitatory; INHIB, inhibitory; ACT, active; PASS, passive; EX, expected; UNEX, unexpected; MVMT, movement; Y, response present; N, no response present.



TRACK DEPTH	SOMATOSENSORY PROPERTIES: TOUCH EXCIT	TOUCH INHIB	DETOUCH EXCIT	DETOUCH INHIB	VIBRATION ACT EX	VIBRATION PASS EX	VIBRATION PASS UNEX	JOINT MVMT ACT EX	JOINT MVMT PASS EX	JOINT MVMT PASS UNEX	RECEPTIVE FIELD FACE	RECEPTIVE FIELD UPPER TORSO	RECEPTIVE FIELD LOWER TORSO	OUT OF SIGHT ACT EX	OUT OF SIGHT ACT UNEX	OUT OF SIGHT PASS EX	OUT OF SIGHT PASS UNEX	IN SIGHT ACT EX	IN SIGHT ACT UNEX	IN SIGHT PASS EX	IN SIGHT PASS UNEX	HABITUATION
EXAMPLE:																						
F115 |25.93|	Y	N	N	N	N	N	N	N	N	N	Y	Y	Y	N	Y	N	Y	N	Y	N	Y	N-20 TRIALS

TRACK DEPTH	VISUAL PROPERTIES: TOWARD	AWAY	TRANSLATE LEFT/RIGHT	UP/DOWN	REACH TOWARD	REACH AWAY	RETRACT	OTHER (SPECIFY)	INHIB	AUDITORY PROPERTIES (SPECIFY)
EXAMPLE:										
F115 |25.93|	Y	N	N	N	Y	N	N	FORM INSENSITIVE	N	N

Appendix C

The results of a short human study make interesting comparison. Twenty human subjects (Psychology students and staff) were asked to rank order the normal stimulus, N, and jumbles, J1-J3, from 1 (the most face-like) to 4 (the least face-like while comparing each test stimulus with a picture of the real monkey that had acted as a subject for the models.

An overall difference in conditions was observed, $Xr\ (3)=40.02$, $p<0.001$ with a Friedman analysis of variance. Using Page's L trend test to compare conditions, a significant trend in the direction N, J3, J2, J1 ($p<0.001$) was revealed, contrary to the order suggested from the monkeys' responses reported in Experiment I. A number of the subjects when asked to comment on their choice of rank order stated that J3 'looked like an upside-down face'.